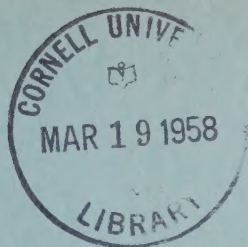


1
A 93
v. 5, no. 4

COMPLIMENTARY COPY



AUSTRALIAN JOURNAL OF ZOOLOGY

VOLUME 5

NUMBER 4

DECEMBER 1957

REGISTERED IN AUSTRALIA FOR TRANSMISSION BY POST AS A PERIODICAL

AUSTRALIAN JOURNAL OF ZOOLOGY

A medium for the publication of results of original scientific research in zoology with special emphasis on the descriptive phases.

Published by the Commonwealth Scientific and Industrial Research Organization.
Issued as material becomes available, 10/- per issue.

BOARD OF STANDARDS

The Board of Standards for this Journal is appointed by the Commonwealth Scientific and Industrial Research Organization and the Australian Academy of Science and consists of Professor J. G. Wood (Chairman), Dr. N. S. Noble (Editor), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor Sir Leslie Martin, and Professor W. P. Rogers.

ADVISORY COMMITTEE

Acceptance of papers for this Journal is in the hands of an Advisory Committee appointed by the Board of Standards and consisting of Dr. N. S. Noble (Chairman and Editor), Dr. H. G. Andrewartha, Dr. A. J. Nicholson, Mr. F. N. Ratcliffe, Professor W. P. Rogers, and Professor H. Waring.

OTHER JOURNALS PUBLISHED BY C.S.I.R.O.

Australian Journal of Physics	}	Issued quarterly, £2 per annum
Australian Journal of Chemistry		
Australian Journal of Biological Sciences		
Australian Journal of Applied Science		
Australian Journal of Agricultural Research	}	Issued six times a year, £2 per annum
Australian Journal of Marine and Freshwater Research		
Australian Journal of Botany	}	Not issued at regular intervals, 10/- per issue

The Organization is a signatory to the Fair Copying Declaration, details of which may be obtained from the office of the Royal Society, London.

All enquiries and manuscripts should be forwarded to:

The Editor,
Australian Journal of Zoology,
Commonwealth Scientific and Industrial Research Organization,
314 Albert Street, East Melbourne, C.2., Victoria

MELBOURNE

BLOOD-SUCKING FLIES (DIPTERA) AND MYXOMATOSIS TRANSMISSION IN A MOUNTAIN ENVIRONMENT IN NEW SOUTH WALES

By D. J. LEE,* A. L. DYCE,† and A. K. O'GOWER*

[Manuscript received July 17, 1957]

CONTENTS		Page
Summary		356
I. Introduction		356
II. Description of the study area—Mt. Flora, near Colo Vale ..		358
III. Outline of proposed studies		262
IV. Outline of the course of the investigations		363
(a) Spring and early summer observations, 1952–53		363
(b) Late summer observations, 1953		363
(c) Spring and early summer observations, 1953–54		364
(d) Late summer and autumn observations, 1954		364
(e) Winter observations, 1954		364
(f) Subsequent observations		364
V. Myxomatosis and the rabbit population		364
VI. Virus-recovery experiments		368
VII. Techniques of collection of biting flies		369
(a) Collections for virus testing		369
(b) Collections for general biological information		370
VIII. List of species of biting flies collected at Mt. Flora		371
IX. Observations on mosquitoes (Culicidae)		372
(a) Oviposition and eclosion		372
(b) Larvae		375
(c) Adults		376
(i) Seasonal abundance		376
(ii) Biting activity		377
(iii) Resting places		381
(iv) Blood sources		383
(v) Distribution in various habitats and at different times of the year		386
(d) Individual species		387
(i)–(iii) <i>Anopheles</i> spp.		387–8
(iv) <i>Tripteroides atripes</i> and <i>Tripteroides</i> sp.		389
(v) <i>Uranotaenia pygmaea</i>		389
(vi) <i>Theobaldia inconspicua</i>		389
(vii) <i>Taeniorhynchus linealis</i>		389
(viii)–(xix) <i>Aedes</i> spp.		389–91
(xx)–(xxiii) <i>Culex</i> spp.		392

* School of Public Health and Tropical Medicine, University of Sydney.

† Wildlife Survey Section, C.S.I.R.O., Canberra.

X. Observations on sandflies (Ceratopogonidae)	..	..	..	392
(a) <i>Leptoconops stygius</i>	..	..	..	393
(b) <i>Culicoides magnimaculatus</i>	..	..	..	393
(c) Other <i>Culicoides</i> spp.	..	..	..	393
(d) <i>Lasiohelea townsvillensis</i>	..	..	..	393
XI. Observations on black flies (Simuliidae)	..	..	..	394
XII. Observations on March flies (Tabanidae)	..	..	..	395
XIII. Observations on Leptidae (Rhagionidae)	..	..	..	395
XIV. Conclusions	..	..	..	396
XV. Acknowledgments	..	..	..	399
XVI. References	..	..	..	399

Summary

The possible vectors of myxomatosis amongst rabbits in a typical mountain environment in eastern New South Wales have been investigated. The disease was established in an isolated population of rabbits and the course of its fluctuations followed through a period of two and a half years, involving two large-scale reductions in rabbit density.

Of over 60 species of blood-sucking flies encountered, 9 species of Culicidae, 2 of Simuliidae, 3 of Ceratopogonidae, and 1 of Tabanidae have been shown to feed on rabbits. Two recoveries of myxomatosis virus have been made from mixed collections of *Aedes queenslandis* and *A. alboannulatus*.

The relative importance of the species known to attack rabbits is discussed in relation to the transmission and maintenance of the disease. Information on host preferences and the feeding, resting, and movement of adults is given. Possible factors influencing the autumn incidence of the disease on the eastern coast and tablelands area of New South Wales are discussed, and further means of exploiting myxomatosis towards the control of rabbits in specific environments are suggested.

I. INTRODUCTION

The investigations embodied in the present paper cover part of the complex problem presented by the experimental introduction of myxomatosis as a controlling factor of rabbit populations in eastern Australia.

After the successful introduction of the disease in 1950, and the initial spectacular outbreak confined to the inland river systems in 1950-51, it soon became evident that useful kills were obtained over a wide climatic and topographic range. Ensuing activity was not confined to the warmer seasons; nor was disease always associated with plagues of blood-feeding insects, hence many problems have arisen as to how the disease was transmitted.

Since its introduction to Australia, the European wild rabbit (*Oryctolagus cuniculus* (L.)) has entrenched itself in a wide variety of habitats. The infested area of New South Wales can be conveniently divided into three distinct regions: the long, narrow coastal plain, the Great Dividing Range, and the extensive western plains. These major divisions of the State present differences in climate and habitat which are reflected in the complex of mosquitoes and other biting flies present in each, the relative abundance of various species, and the overall population levels of these insects.

The magnitude of the disease-transmission problem was such that a complete coverage of all types of outbreaks in all the districts in which these occurred was impracticable. One type of area which did not come under early observation was the mountain habitat, especially near the headwaters of coastal streams. Accordingly it was decided to investigate the incidence of disease, and the means of transmission, in an area of this type.

Because of the known differences of the mosquito fauna of such areas from that of the western plains and waterways, it was felt that little could be predicted as to the possible success of myxomatosis in the rabbit-populated sections of the mountain zone. In particular it was felt that the coastal-stream headwaters were decidedly marginal for myxomatosis transmission in the sense that here mosquito populations



Fig. 1.—Map of New South Wales indicating the position of Colo Vale relative to the Great Dividing Range and the coastline.

seldom, if ever, reached a noticeably high density, with, consequently, considerably decreased opportunities for contact between rabbits and mosquitoes. Furthermore, certain species regarded as successful vectors of myxomatosis along the western rivers also occur on the coast and in the Dividing Range, but in such small numbers that it was believed there must be other major vectors present if myxomatosis were to be useful as a means of rabbit destruction in these mountain valleys and slopes.

In September 1952 the Colo Vale area was selected as a convenient and favourable one for the type of investigations contemplated. This had a high rabbit population with no previous history of myxomatosis and the mosquito population was thought to be restricted in species present and in density, and uncomplicated by the presence of most other biting flies.

The area was surrounded on all sides by country quite unsuitable for maintaining sizeable rabbit populations. This isolation was of the order of 3 miles to the south-east and much greater in all other directions, thus permitting the assumption that local fluctuations in rabbit numbers would not be influenced by happenings in populations outside the study area.

Having located such an area we proposed to introduce myxomatosis, await evidence of its spread, and then determine, by whatever means we could, the vector or vectors responsible.

II. DESCRIPTION OF THE STUDY AREA—MT. FLORA, NEAR COLO VALE*

The selected area, situated about 80 miles south-west of Sydney and a few miles north of Mittagong, is approached through the small village of Colo Vale (see Figs. 1 and 2). Locally the area is known as Mt. Flora and it forms part of the upper catchment of the Nattai R. Mt. Flora is an isolated cleared area comprising several farms now largely devoted to dairying, with small areas of cultivation for winter fodder. The total cleared area and the marginal rabbit-populated forest comprise roughly 2000 acres (see Fig. 3).

Although surrounded by typical rugged Hawkesbury sandstone cliffs and gullies, the area itself is an alkaline trachyte intrusion and considerably more fertile than the country which surrounds it. The trachyte plug is continuous from the highest point of the land (2434 ft) to the bed of the Nattai R. at approximately 1250 ft.

At one time the greater part of the area was covered with dry sclerophyll eucalypt forest but this was cleared for grazing many years ago. Residual trees remain but most of the existing timber dividing the clearings is either regrowth or untouched forest in the creeks or on rocky outcrops. In places certain plant species dominate and sometimes these form habitats of special significance.

On the slopes, isolated thickets of paper-bark (*Melaleuca styphelioides* Sm.) are often the only areas with an appreciable canopy. Elsewhere on the slopes, regrowth (*Eucalyptus* and *Acacia* spp.) or original forest is associated with moderately dense ground cover provided by *Stypandra glauca* R.Br. or *Olearia viscidula* Benth.

In Rocky Creek the low, closed canopy is largely provided by *Backhousia myrtifolia* Hook & Harv. and the ground cover by the herringbone ferns, *Pellaea falcata* (R.Br.) Fée and *Doodia aspera* R.Br. Stockyard Creek, on the other hand, has largely grassy banks, with one fairly extensive bracken patch, and the thin canopy provided by the she-oaks (*Casuarina cunninghamiana* Miq.) is high above ground level.

The tops of the hills (Mt. Flora and the even higher adjacent peak Mt. Blatch) are practically bare of trees but are grass-covered and with no surface water. The saddles below these are relatively bare, grassed, and with varying degrees of shelter around the three homesteads and dairy yards. Here, however, water is present in tanks and dams. Both the tops of the hills and the saddles are exposed from the north-east to the south-east with views encompassing a distance of some 40 miles. From this level, stony ridges alternate with grassy depressions through which

* Photographic studies of the area, and of specific habitats, are presented, with explanatory captions, in Plates 1 and 2.

juvenile creeks drain storm-water, but normally surface water is absent. Most of the grazing land is in this section of the area, although small portions are covered with eucalypt regrowth, limited patches of bracken and blackberry, and paper-bark thickets.

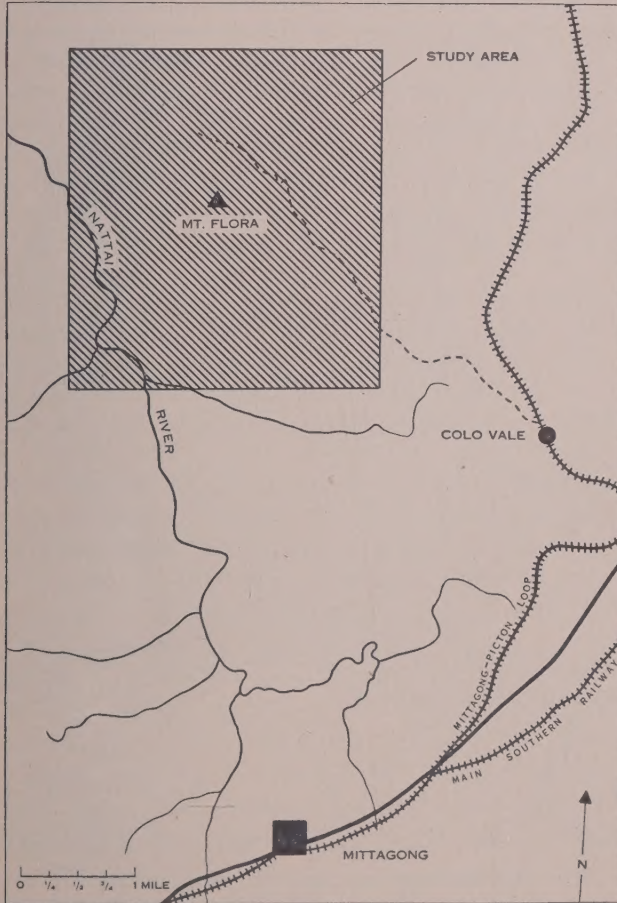


Fig. 2.—Position of the study area in relation to nearby townships and the Nattai River.

Below this level the creeks become patent with semi-permanent to permanent water with varying degrees of regrowth or natural forest between. Some creeks are only shallowly excavated and consist of a chain of small exposed rock-pools. Others are deeply excavated in rock (Rocky Creek). Another (Stockyard Creek) is partly rocky, but runs more characteristically through alluvial deposits. Here and there seepages occur which contribute to the permanency of the creeks, and at times form small boggy areas. Later these creeks either disappear in ti-tree marsh or fall over rugged waterfalls, followed by further steep rocky drops with rather larger pools before they become normal surface-running streams discharging into the Nattai R.

Apart from three (more recently four) excavated earth tanks, a few soakage holes, and very limited other artificial breeding grounds (tanks and wells), these creeks provide all the mosquito breeding habitats for the area exclusive of temporary breeding grounds and tree-holes.

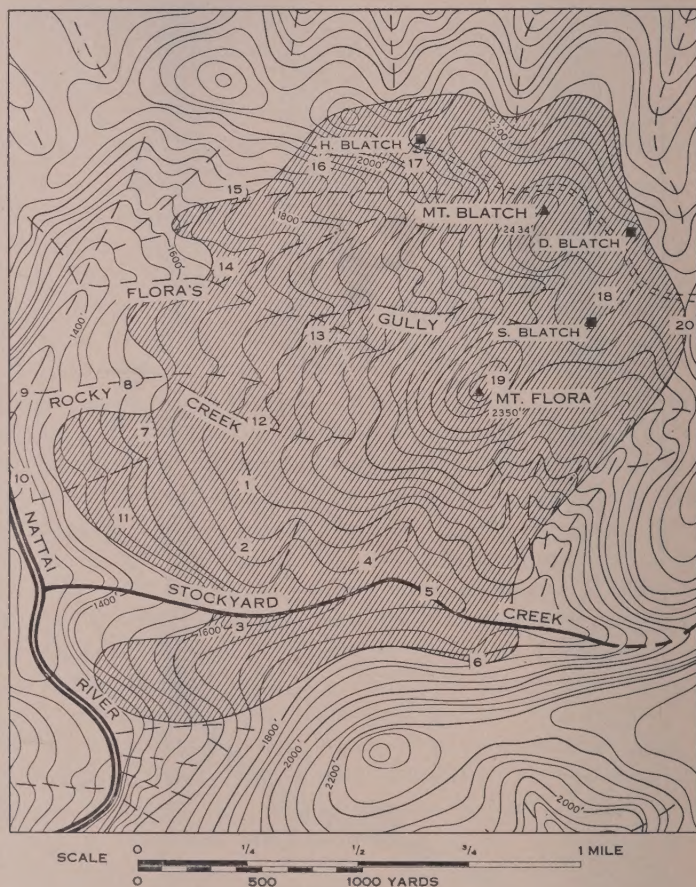


Fig. 3.—Details of the study area. The hatching indicates the approximate limits of the rabbit infestation. Special sites mentioned in the text are indicated by numbers. Such sites were used as observation points repeatedly and were intended to give a cover of the variety of habitat types in the area. Exploratory activities were not confined to the sites indicated but were often continuous between the various numbered points. 1, the area around an unused house and milking shed. This is a fairly open gently sloping grazing area with incipient creek formation giving abundant temporary breeding sites after rain. A number of open tanks and a well, all associated with the buildings, supported a continuous larval mosquito population. 2, this is one of the timbered ridges frequently utilized for evening ridge collections. 3, Stockyard Creek crossing. 4, the location of one of the largest ti-tree thickets. 5, Upper Stockyard Creek. 6, heavily timbered zone with thick undergrowth on the steep slope at the base of the sandstone escarpment.

[For continuation see opposite page.]

The area supports cattle, sheep, a few horses, and, at the time of our initial observations, there was a heavy rabbit population. Possums (*Trichosurus vulpecula vulpecula* (Kerr) and *Pseudocheirus laniginosus laniginosus* (Gould)), gliders (*Acrobates pygmaeus pygmaeus* (Shaw), *Petaurus breviceps breviceps* Waterhouse, *P. norfolcensis norfolcensis* (Kerr), and *Schoinobates volans volans* (Kerr)), kangaroos (*Macropus canguru major* Shaw and *M. robustus robustus* Gould), wallabies (*Protemnodon bicolor bicolor* (Desmarest) and *P. rufogrisea banksiana* (Quoy & Gaimard)), wombats (*Phascolomys mitchelli mitchelli* Owen) also occur together with smaller terrestrial animals such as pouched mice (*Antechinus flavipes flavipes* Waterhouse) and the allied rat (*Rattus assimilis assimilis* (Gould)). Snakes (*Pseudechis porphyriacus* (Shaw), *Demansia textilis* (Dum. & Bibr.), *Denisonia superba* (Gunther) and others) and lizards (*Varanus varius* (Shaw), *Physignathus leseurii* (Gray), *Sphenomorphus quoyi* (Dum. & Bibr.), *S. taeniolata* (Shaw) and others) are abundant in the creeks, and a wide variety of bird life is also present.

Climatically the area is regarded (Department of Lands 1946) as being borderline between one zone having no marked seasonal drought and a mean annual rainfall of 25–40 in., and another zone having a seasonal drought of from 2 to 4 months occurring in winter–spring and a mean annual rainfall of 20–35 in. The mean temperature for the hottest month of the year is given as greater than 72°F and the coldest was 46–55°F.

Accurate rainfall records have not been kept at Mt. Flora itself, the nearest available records being for Colo Vale, c. 4 miles away. For the purpose of general seasonal rainfall, there should be no significant difference between the two, although with storm-rains individual falls might vary within that distance.

The average annual rainfall for the 12 years 1943–54 is over 41 in., the lowest annual total being 21.30 and the highest 68.84 in. The detailed records for Colo Vale, over the period of our observations (1952–55) are recorded as weekly and monthly totals in the histograms presented in Figure 4.

Because of the rather abrupt fall in altitude through the study area, prevailing conditions of temperature and wind vary fairly markedly. The higher elevations tend to be bleak and windy because of their degree of exposure; lower down the slopes milder conditions prevail and there is considerable protection from both southerly and

7, the ridge between site 1 and Rocky Creek, frequently used for evening collections. 8, Rocky Creek: this was the section studied most intensively. 9, Lower Rocky Creek at the point where continuous flow is established in a rather deep narrow cutting. 10, the bank of the Nattai R. There is a large ti-tree swamp in this area. 11, a very rocky area at the commencement of the steep gradient to the Nattai R. 12, Upper Rocky Creek. Permanent seepages with some emergent vegetation. 13, a creek crossing with permanent seepage. This was a convenient observation point on the only roadway through the area from site 17 to site 3. 14, an open creek junction with permanent water, blackberry, and bracken patches surrounded by open grasslands. 15, an incipient watercourse with infrequent small earth pools with overhanging banks. This area gets little direct sunlight. 16, a steep grassy slope with occasional trees leading directly from a creek to the top of the ridge. 17, an inhabited farmhouse with a well, tanks, and small dam. 18, this area has the three major excavated dams and drains to Upper Stockyard Creek. 19, the steep crest of Mt. Flora. The small polluted dam in a sheepyard lies at the base of the crest. 20, the point at which entry is made to the study area from the plateau top.

westerly winds, which, in this general area, are respectively the dominant cold and drying winds.

III. OUTLINE OF PROPOSED STUDIES

As mentioned above, the initial project was to be an attempt to determine whether myxomatosis would become established in an area such as this and, if so, which mosquito species acted as vector. Should it become established its course was

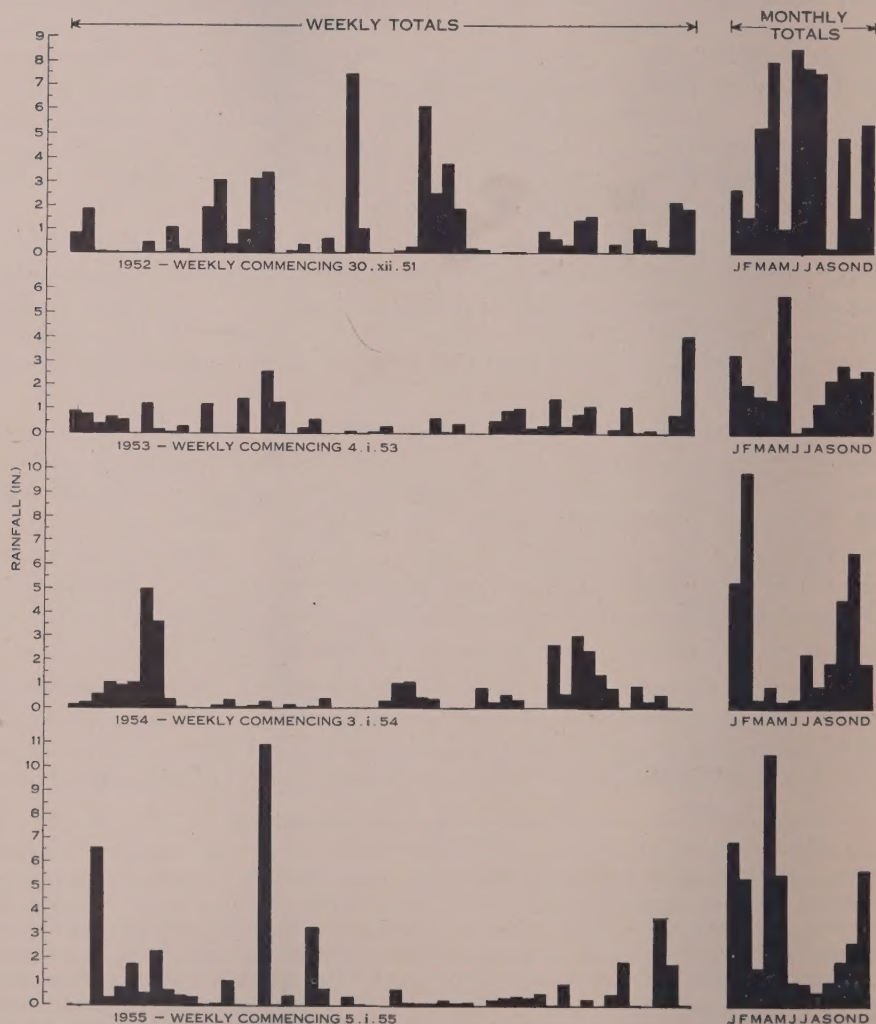


Fig. 4.—Histograms showing weekly and monthly rainfall totals (weekly totals commence from the nearest Sunday to January 1; monthly totals are for calendar months).

to be followed, mosquito activity was to be investigated, and if possible a correlation between disease and mosquito activity revealed. Priority was to be given to the

recovery of myxomatosis virus from wild-caught mosquitoes but other relevant points were to be investigated as opportunity offered.

In developing techniques for recovering wild mosquitoes we inevitably learned a great deal about their behaviour and feeding habits. Further, as work proceeded, it became obvious that observations on the habits and activity of other biting flies (Ceratopogonidae, Simuliidae, Tabanidae, and Leptidae) present in the area would need to be made in order to arrive at any appreciation of the relative importance of any of the varied range of potential rabbit-feeding insects.

IV. OUTLINE OF THE COURSE OF THE INVESTIGATIONS

(a) *Spring and Early Summer Observations, 1952-53*

Entomological observations in this period were largely confined to mosquito larval habitats and breeding potentialities. These confirmed our initial assumption that the *Aedes alboannulatus** complex was dominant in the area. Next in importance appeared to be *Anopheles annulipes* and *Aedes notoscriptus*. Other species found breeding were *Culex pipiens australicus*, *C. pseudomelanoconia*, and *C. cylindricus*.

Of these species the members of the *A. alboannulatus* complex were found to occur in almost all of the observed larval habitats (see Table 4). Taking into account the relative abundance of different types of breeding habitats and their degree of population by mosquito larvae, it was considered that the *A. alboannulatus* complex would have to prove efficient vectors of myxomatosis if any major epizootic were to occur. Rabbit observations were initiated and the introduction of myxomatosis effected.

(b) *Late Summer Observations, 1953*

The primary objective during this period was the collection of adult mosquitoes for virus recovery.

Three visits were made to the area, the first in mid-February, the second in the second week of March, and the third during the second week of April. Preliminary observations during this period established the different types of habitats from which adult mosquitoes could be collected and the most useful methods of collection in an area of this kind. Both sandflies (Ceratopogonidae) and March flies (Tabanidae) were also caught.

The collections made on the second occasion resulted in a recovery of virus from mosquitoes caught over the extent of our study area. On the third occasion segregation of catches for the major habitat differences (creek collections as against

* In the early stages of this investigation, we considered that the closely related forms or species of the complex comprising *Aedes alboannulatus*, *A. occidentalis*, and *A. occidentalis* var. *milsoni* as conventionally identified at that time were all so similar in their general ecology that little purpose would be served by studying them individually. Furthermore, the conditions of collection of adult mosquitoes for virus recovery and the need for speed in sorting collections to species made it impracticable, at that time, to segregate the components of the complex. Later, when striking ecological differences between *A. alboannulatus* and *A. queenslandis* (a name it was found necessary to take out of synonymy to cover the dominant form in the eastern States which had been commonly identified as *A. occidentalis* since the work on Australian mosquitoes by Edwards (1924)) were observed, it became essential that these two should be studied individually.

ridge collections) was also undertaken in an attempt to localize the virus transmission to a particular environment. However, as no virus was recovered, this was unsuccessful.

(c) *Spring and Early Summer Observations, 1953-54*

The primary objective of the first visit for this season (end of September) was to observe the effect of myxomatosis on the rabbit population and to obtain rabbits for immunity tests. A second visit was made in the latter half of November when an attempt was made to confirm some of the observations made earlier in the year. The dispersal of adult mosquitoes, their characteristic biting times, and the effects of meteorological conditions on biting activity were investigated. An attempt was also made to obtain more information about other blood-sucking flies which attack rabbits.

(d) *Late Summer and Autumn Observations, 1954*

The area was visited once each month from the middle of February until the end of May, similar observations being undertaken. Further, the ecological differences of the two species, *A. alboannulatus* and *A. queenslandis*, were studied in more detail. Investigations of larval habitats were also expanded, and greater efforts were made to disclose the characteristic resting places of the local mosquitoes.

(e) *Winter Observations, 1954*

As a virtual cessation of mosquito activity during the winter months was considered improbable the area was visited twice during June and July and collections made using techniques identical with those previously employed.

(f) *Subsequent Observations*

Visits to the area continued from the spring of 1954 through to the winter of 1956. The work undertaken on some of these occasions was not related to the studies herein reported. Wherever such subsequent observations have added to our understanding of mosquito activity, or myxomatosis incidence, due cognisance of this has been taken in the writing of the various sections.

V. MYXOMATOSIS AND THE RABBIT POPULATION

The initial introduction of the disease was made with the help of the District Rabbit Inspector, Mr. S. Elrlington, and others, on October 9 and 10, 1952, when 23 local rabbits were caught, inoculated, and released. Further inoculations were carried out early in December. Dried virus supplied by the Glenfield Veterinary Research Station, N.S.W., was used. This is not known to differ from the original Martin B strain used to initiate the widespread epizootic of 1950-51. These inoculations were successful in establishing the disease, which was later seen in all parts of the area.

During the period from December 1952, when the first natural cases of the disease were seen, to the end of April 1955, myxomatosis activity showed three clearly defined phases. The first was one of extended disease activity, at low to moderate intensity, which, by October 1953, augmented by the activity of a trapper, resulted

in an estimated 95 per cent. reduction in the rabbit population. During the second phase of nearly 18 months—from October 1953 to February 1955—the disease was quiescent, and for the greater part of this period, i.e. until breeding started in September 1954, rabbit numbers remained very low. The third phase consisted of a build-up in disease activity from February 1955 to a spectacular “explosive” epizootic during March and April.

When a myxomatosis outbreak takes the form of prolonged, low-intensity activity rather than a sharp, well-defined epizootic, experience in other areas has shown that the effects are difficult to follow in detail and to assess. This proved to be the case during the first phase of myxomatosis activity at Mt. Flora, where conditions for observing the rabbit population were far from ideal. An estimate was desired, even if only a rough one, of the changes in rabbit population density and of the intensity of disease activity. To this end, observations were made periodically along a standard route. This route was between 1 and $1\frac{1}{4}$ miles long, and traversed the most densely rabbit-populated part of the area. The route was walked slowly, and all rabbits seen were counted. Field-glasses were used, and usually more than one count was made during each visit, always in the early morning or late afternoon, the expected peaks of the animals' above-ground activity. The counts were made on most occasions by the same person, in the same manner, precautions being taken not to disturb the rabbits unduly.

TABLE 1
RABBIT SIGHTINGS ON STANDARD ROUTE

Month	No. of Counts Made	Average No. of Rabbits Seen	Average No. of Sick Rabbits
October 1952	2	120	Nil
November 1952	2	117	Nil
February 1953	3	109	6
March 1953 (cold, windy rainy weather)	1	84	6
April 1953	2	140	2
September 1953	1	4	Nil
November 1953	2	5	Nil

The results of the standard route counts are set out in Table 1. They can, of course, provide no more than a rough indication of the changes in the rabbit population and in disease activity that occurred during the period covered, but we believe the indication to be a useful one. The observations along the standard route were discontinued after November 1953, as the rabbit population remained at such a low level that daily counts by three or more observers seldom reached a total of even two figures. In addition to the standard counts recorded, one was made along a different route at the end of the first week in January 1953, in which six sick rabbits in a total of 300 were noted.

An interruption in observations between April and September 1953 makes it necessary to resort to a certain amount of conjecture in reconstructing the progress

of the disease during the first twelve months after the release of the infection. The transect counts indicate that the main kill, at any rate in that part of the area covered by the standard walk, took place after April; and no general reduction in rabbit numbers during the preceding months was obvious to us. On the other hand, the observations of local residents, which supplemented our own and were more comprehensive in certain respects, indicated that a noticeable reduction in rabbit numbers had begun during the early months of 1953, with some foci of intense disease activity developing late in January. Thus out of 20 rabbits observed on one of the higher slopes 10 were infected, and at about the same time the paddock on the top of the second highest cleared hill (Mt. Flora itself) was virtually cleaned up. The only successful recovery of virus, from mosquitoes collected in March, also suggests that transmission built up to a peak of intensity before April. Moreover, an increase in the activity of crows during midsummer provided indirect evidence of greater disease incidence in the area than we were able to observe. (No intensification of the activity of carrion-eating birds was observed during the following summer, but it was again obvious during the epizootic period of 1955.)

From May until October 1953, a trapper worked intermittently on the area and removed some 2000 rabbits. During this period sick rabbits were taken in the traps from time to time up to the end of August. The Mt. Flora trapper was exceptional in his willingness to continue operations on a dwindling rabbit population, right up to the time when the numbers were at such a low level that further activity was completely unrewarding.

Between October 1 and 3, 1953, the first of two samples of rabbits collected in the area for blood tests was obtained by night shooting and trapping. The sample was collected over at least half the width of the area, and comprised 19 adults and two kittens. Excluding the kittens, which were susceptible, six of the animals (31.6 per cent.) proved to be recovered immunes. This figure is comparable with the incidence of immunity shown by Fenner, Marshall, and Woodroffe (1953) in the rabbit population following the initial, prolonged epizootics in the area around Moree, N.S.W., which produced an estimated mortality of the order of 90 per cent.

The progress and performance of the disease during the twelve months following its release can be summed up as follows. Soon after the first sighting of sick rabbits in December 1952, the infection became dispersed widely throughout the study area—a dispersal that involved vector movements of over a mile in places, and an altitudinal spread of 600 ft over gradients of 1 in 5. Then followed a period, lasting until October 1953, of long, drawn-out disease activity of low average intensity, such as has been recorded in several parts of eastern Australia, particularly during the first spread of myxomatosis. Foci of high-level activity, developing in different parts of the area at different times, seem to have been important at Mt. Flora; and it is probable that such a pattern of activity underlies most seemingly uniform, low-intensity but ultimately effective outbreaks. It is possible also that this might be associated with minor movements and concentrations within the rabbit population, stimulated by local changes in the quantity and attractiveness of available feed and, at Mt. Flora, by trapping operations.

An overall reduction in rabbit numbers of approximately 95 per cent. is indicated by the transect counts; and this tallies with the observed difference in

rabbit density over the whole area in the spring of 1953 as compared with the spring and early summer of the preceding year, a difference which was associated with a marked improvement in the pasture and increase in the milk yields. An estimate of the actual number of rabbits killed by myxomatosis hinges on certain assumptions regarding the initial (1952) population density. We feel confident, from our knowledge of other rabbit-infested areas, that the 1500 acres in the study area was originally carrying an average of at least three rabbits per acre, and possibly as many as five. On the basis of the lower estimate, with an original total of some 4500, the trapper's toll of a round 2000, and between 200 and 250 survivors, myxomatosis would have accounted for just over 2000 rabbits—approximately the same number as were trapped. If the original density was five rabbits per acre, giving a total population of 7500, over 5000 would have been killed by the disease.

The essential facts regarding the second phase of myxomatosis activity at Mt. Flora have already been given. During the period from October 1953 to September 1954, sightings of rabbits in daylight hours became progressively less frequent, there having been no noticeable recovery in the population as a result of breeding in the spring and early summer. Sick animals were occasionally seen by the residents of the area, indicating that despite the extremely low rabbit population density the infection was managing to persist locally. The last sighting of a sick rabbit during 1954 occurred in early June.

The third phase of myxomatosis activity was preceded by a period of breeding and rapid population build-up, starting in September 1954, with no overt signs of disease incidence. The rabbit population never attained a density comparable with that of 1952; but by February 1955 numbers were sufficiently high for the residents to prepare for a campaign of destruction, in which they were forestalled by the development of an epizootic.

No further inoculations of the virus were made. Infected rabbits (the first encountered since the June sighting mentioned above) were caught on February 7 and 9, 1955, and more were seen on March 19. During the last week of this month and on the first 2 weeks of April, disease activity built up to a peak of intensity, a spectacular epizootic developing which ran its course within 5 weeks. As many as eight sick animals could sometimes be seen from one spot, and the odour of dead rabbits was quite obvious in and around warrens. The ultimate reduction in rabbit numbers was so great that it was impossible to obtain a post-epizootic sample of rabbit sera for antibody tests.

Fortunately a rabbit sample was collected during the period of February 9 to 11, shortly before the development of the epizootic. Of the 30 rabbits trapped, only one (3 per cent.) proved to be immune.

Three groups of virus samples were recovered from Mt. Flora for virulence test. Samples collected on March 12, 1953, February 9, 1955, and April 2, 1955, gave survival times of 19.2, 17.0, and 28.8 days respectively, when tested by the standard technique developed by Fenner and Marshall (1957) in which virulence is assessed by the mean survival time in groups of five fully susceptible laboratory rabbits. As the survival time for the strain of the virus liberated in 1952 is 11 days, it is obvious that a degree of attenuation has taken place in the area. The survival times of the Mt. Flora

samples are in line with those given in tests by the slightly attenuated field strains that have become dominant in south-eastern Australia between 1952 and 1955, and which appear to be associated with a case mortality rate of about 90 per cent.

In its myxomatosis history Mt. Flora thus conforms to the general pattern of the south-coastal region of New South Wales, where outbreaks of the disease tended first to be very patchy and irregular, with the first widespread and effective activity occurring in the 1954-55 season in the form of clearly defined, intense late summer and autumn outbreaks.

TABLE 2
DETAILS AND RESULTS OF ATTEMPTED VIRUS RECOVERY

Date	Species	No.	Batches Tested	Results
February 1953	<i>Aedes alboannulatus</i> }	166	8 (7 × 20, +26)	Negative
	<i>A. queenslandis</i> }			
	<i>A. notoscriptus</i>	26	1	Negative
	<i>Anopheles annulipes</i>	12	1	Negative
	Tabanidae*	12	1	Negative
	(comprising 1 <i>Dasybasis oculata</i> , 6 <i>D. circumdata</i> , and 5 <i>Scaptia xanthophyllis</i>)			
	<i>Culicoides magnimaculatus</i>	95	2 (45 + 50)	Negative
March 1953	<i>Aedes alboannulatus</i> }	313	3 (each c. 100)	2 batches positive
	<i>A. queenslandis</i> }			
	<i>A. notoscriptus</i>	51	1	Negative
	Tabanidae*	63	1	Negative
	(specimens destroyed before they could be identified)			
	<i>Culicoides magnimaculatus</i>	153	2 (each c. 90)	Negative
April 1953	<i>Aedes alboannulatus</i> }	464	9 (each c. 50)	Negative
	<i>A. queenslandis</i> }			
	<i>A. notoscriptus</i>	39	2 (16 and 23)	Negative
	<i>Culex annulirostris</i>	54	2 (15 and 39)	Negative
	<i>Anopheles annulipes</i>	4	1	Negative
	<i>Culicoides magnimaculatus</i>	63	1	Negative

* In virus tests with Tabanidae only, mouthparts were utilized.

VI. VIRUS-RECOVERY EXPERIMENTS

Activities in the late summer and autumn period of 1953 were concentrated on the collection of all possible blood-sucking flies in an attempt to recover myxomatosis virus. Almost all mosquitoes and all March flies collected for this purpose were taken on human bait. A limited number of mosquitoes was recovered from resting places.

Most of the insects were collected in suction tubes (March flies in test tubes) and anaesthetized over ether fume before sorting, which was done on the day of collection. After sorting the insects were placed in corked tubes held in thermos flasks containing ice, this being renewed as required until the material reached the testing laboratory.

Results of these collections are shown in Table 2. Virus was recovered from two batches of mixed *A. alboannulatus* and *A. queenslandis* taken during the month of

March. Results for other species and other months were negative. The possible significance of these findings is discussed later under the individual species involved.

VII. TECHNIQUES OF COLLECTION OF BITING FLIES

(a) Collections for Virus Testing

For the recovery of myxomatosis virus from wild-caught mosquitoes it is important to capture those which are most likely to have already fed on rabbits. For this reason catching outside the range of the rabbit population was regarded as undesirable, as was collection in the vicinity of mosquito breeding grounds where a large proportion of individuals ready for their first blood meal could be expected. Though collections were made near larval habitats and just outside the area of rabbit infestation on most afternoons, catches from the ridges, away from larval habitats and within the rabbit area, especially during the period of dusk activity, were considered more important. However, later observations disclosed that collections adjacent to breeding grounds did include a small percentage of individuals already engorged.

The technique usually used in virus recovery from arthropod vectors involves the indiscriminate collection of suspects, irrespective of their probable degree of contact with the vertebrate hosts. It was of interest to determine whether more selective collection of small numbers of mosquitoes would lead to virus recovery. Two recoveries of myxomatosis virus from a total of 1116 mosquitoes tested in 28 batches shows this selective technique to be practicable and worthy of wider trial. To obtain collections with a high ratio of individuals likely to be of significance the following types of collection were attempted.

(i) *Natural Shelters*.—Collection of adults from such types of natural shelter as rock crevices, stumps, cavities in tree-trunks, and rabbit warrens had not proved very successful in the 1952 spring. Subsequent collections in the following autumn indicated that no useful purpose would be served by persevering with these techniques as a means of mosquito recovery for virus testing although Myers, Marshall, and Fenner (1954) obtained a number of virus recoveries from mosquitoes taken in warrens. Since there might have been some discrepancy between the techniques employed by ourselves and those of Myers, we later took the opportunity of having Myers employ his own techniques for warren recoveries in the Mt. Flora area. As a result of his attempts we still lack any evidence that warren resting is indulged in to any significant degree in an area where abundant alternative resting places in vegetation are available.

(ii) *Domestic Shelters*.—These proved of little use. Some morning recoveries of adults were made from a shed and an unused dairy but these were mainly recently emerged specimens from adjacent domestic breeding places (a well and a tank). Other similar shelters were available but were in very exposed situations on the tops of hills and yielded nothing.

(iii) *Light-traps*.—Both sunrise light-traps of a modified Du Toit pattern and mercury vapour traps were tried, but evening temperatures were usually too cool for light-traps to be really effective. Their major value was to add to the number of species of Ceratopogonidae recorded from the area, although occasional Chironomidae and Simuliidae were also taken.

(iii) *Net Sweeping*—This was sometimes employed over vegetation and was productive of *Ceratopogonidae*.

(iv) *Animal Bait*—Limited trials using calf, horse, dog, and rabbit showed so little promise that the method was not pursued until a later stage when more attention could be devoted to it.

(v) *Human Bait*—The use of man as bait gave early indications of being the most successful technique so efforts were concentrated in this direction.

Collectors worked as a group, usually seated some yards from one another, or at times in pairs, and the legs were exposed from the knees down to attract mosquitoes.

In the mornings, collections were made at various places along the slopes on either side of Steady Creek (sites 3-6, Fig. 3). In the afternoons collections were made on the banks at head of Rocky Creek (site 8, Fig. 3) which contained a limited series of important breeding pools. Early evening catches were from ridges between the above two areas (sites 2 and 7, Fig. 3). An attempt was thus made to collect over a reasonably wide area in the mornings and evenings within the rabbit-populated area and in afternoons just on its fringe.

At each site collectors would sit down for at least 15 min. Usually no attack would be noticed until 5-10 min after sitting down. If any mosquitoes came, the collectors would remain until the attack ceased before moving to another site. Such was the plan of operation in the mornings. Afternoon collections were confined to a section of Rocky Creek where a prolonged period of catching was usually required and no movement of the collector was necessary. In the evening, collectors remained in the same places, usually on ridges, from 1730 hr or thereabouts until the biting wave occurred and subsided, which was within the next 2 hr.

(b) Collection for General Biological Information

Since any blood-sucking insects caught contributed to the general body of information sought, techniques following the early preoccupation with the recovery of virus were far less restricted.

In particular, natural shelters were explored, light-trapping was carried out in a variety of habitats, and a series of animal bait trials were attempted. Collections from human bait were continued on all possible occasions.

Reflecting on our adult collections made in these ways we found it impossible to ignore three important side issues.

- (i) That a far more comprehensive picture of the biting-fly complex was gained, particularly in the case of *Tabanidae*, than that obtained from larval searching. This was further support for the general contention that more significant data are revealed by a concentration on adult collections rather than the more popular larval surveys, especially in the mosquito field. Other groups taken as adults attracted to human bait were *Ceratopogonidae*, *Simuliidae*, *Tabanidae*, and *Leptidae*.
- (ii) That patterns of behaviour may be incidentally revealed by such collecting.
- (iii) That recently emerged specimens of mosquitoes and other blood-sucking Diptera may still be collected from man and yield information on natural biting habits.

VIII. LIST OF SPECIES OF BITING FLIES COLLECTED AT MT FLORA

(a) *Culicidae* (blood-sucking species only)

1. *Anopheles* (*Anopheles*) *stigmaticus* Skuse
2. *Anopheles* (*Anopheles*) *atratiipes* Skuse
3. *Anopheles* (*Myzomyia*) *annulipes* Walker
4. *Tripteroides* (*Mimecomyia*) *atripes* (Skuse)*
5. *Uranotaenia pygmaea* Theobald
6. *Theobaldia* (*Culicella*) *inconspicua* Lee
7. *Taeniorhynchus* (*Cogallitidia*) *nasalis* (Skuse)
8. *Aedes* (*Mucidus*) *alternans* (Westwood)
9. *Aedes* (*Chaetocoelomyia*), sp.
10. *Aedes* (*Finlaya*) *quasiatritractor* (Theobald)
11. *Aedes* (*Finlaya*) *retosorigens* Skuse
12. *Aedes* (*Finlaya*) *mallochi* Taylor
13. *Aedes* (*Finlaya*) *albocinctus* Macquart
14. *Aedes* (*Finlaya*) *queenlandis* (Strickland)
15. *Aedes* (*Finlaya*) *biocellatus* (Taylor)
16. *Aedes* (*Finlaya*) *monocellatus* Marks
17. *Aedes* (*Finlaya*) *subauriferum* Marks
18. *Aedes* (*Ochlerotatus*) *burpengaryensis* Theobald
19. *Aedes* (*Ochlerotatus*) *flavifrons* Skuse
20. *Aedes* (*Ochlerotatus*) *macbryani* Mackerras
21. *Aedes* (*Ochlerotatus*) *nivalis* Edwards
22. *Aedes* (*Ochlerotatus*) *subtricolor* (Macquart)
23. *Aedes* (*Ochlerotatus*) *super* Skuse
24. *Aedes* (*Ochlerotatus*) *theobaldi* Taylor
25. *Aedes* (*Ochlerotatus*) *rigilar* (Skuse)
26. *Aedes* (*Ochlerotatus*) *super* Skuse
27. *Aedes* (*Pseudobursa*) *brachymerus* Edwards
28. *Culis* (*Leptocryptus*) *elysius* Theobald
29. *Culis* (*Culis*) *condictus* Skuse
30. *Culis* (*Culis*) *formosus* Wiedemann
31. *Culis* (*Culis*) *gravis australis* DeMeillon, Worsky & Drummond
32. *Culis* (?) *Culis* *postparvicornis* Lee
33. *Culis* (*Neoculis*) *pergandei* Taylor
34. *Culer* (*Neoculer*) *pseudomelanocornia* Theobald

(b) *Ceratopogonidae* (blood-sucking species only)

1. *Leptocnops stygius* Skuse
2. *Lasiocheila roussetiensis* Taylor
3. *Culicoides magnimanus* Lee & Reye
4. *Culicoides parvicornis* Lee & Reye
5. *Culicoides bancrofti* Lee & Reye
6. *Culicoides antennalis* Lee & Reye
7. *Culicoides marksi* Lee & Reye
8. *Culicoides dycei* Lee & Reye
9. *Culicoides austropalpis* Lee & Reye
10. *Culicoides nattaensis* Lee & Reye†

(c) *Simuliidae*

1. *Austrosimulium furiosum* (Skuse)
2. *Austrosimulium bancrofti* Taylor
3. *Simulium melatum* Wharton
4. *Simulium ornatipes* Skuse
5. *Simulium* sp. (*clathrinum* group)
6. *Cnephia* spp. (two species)

(d) *Tabanidae*

1. *Dasypasis circumdata* (Walker) (both typical and dark form)
2. *Dasypasis insignis* Taylor (both typical and varietal form)
3. *Dasypasis neobasalis* Taylor
4. *Dasypasis penilis* (Erickson)
5. *Dasypasis minorata* (Ferguson & Hill)
6. *Dasypasis melana* Bancroft
7. *Scaptomyza insignis* (Ferguson)
8. *Scaptomyza fusca* (Donovan)
9. *Scaptomyza subtypica* (Macquart)
10. *Upharocera minorata* Taylor
11. *Cyrtomyza* sp. (undescribed)

(e) *Leptidae* (Ring-billed)

1. *Spaniopis longicornis* Ferguson
2. *Spaniopis minor* Ferguson

* At least one other species of *Tripteroides* occurs in the area but has been inadequately collected.

† Two other as yet undescribed species of *Culicoides* have been collected in the area.

IX. OBSERVATIONS ON MOSQUITOES (CULICIDAE)

(a) Oviposition and Eclosion

Eggs which subsequently hatched typical *A. queenslandis* larvae were found on the cement-rendered lining of an open-topped domestic rainwater tank. Although quite unnatural, this site appeared to be most suitable for the oviposition of this sylvan species as many thousands of eggs were present. When first located on February 19, 1954, the singly placed eggs were separated into discrete horizontal bands which encircled the tank lining, each band being not more than $1\frac{1}{2}$ in. wide. The density of eggs along each band increased with increasing roughness of the cement surface and was highest where cavities of $1/16$ in. were frequent.

Eggs in the lower band were confined to the damp surface immediately above the water-line. They were shining black and turgid whereas eggs in other bands on the dry cement surface above were dull and collapsed. Turgid egg samples subjected to air drying at room temperatures for 7 days also collapsed and such eggs were found to be incapable of hatching.

TABLE 3
HATCHING IN TAP WATER OF AEDES QUEENSLANDIS EGGS COLLECTED
MARCH 24, 1954 FROM A MOIST CEMENT SURFACE AND STORED ON DAMP
FILTER PAPER

Egg Batch	Date Immersed in Tap Water	Date of Hatching	No. Hatched	Date Discarded
4	24.vi.54	12.vii.54	3*	8.ix.54
		14.vii.54	5	
		15.vii.54	3	
		16.vii.54	1	
		7.viii.54	4	
5	29.vii.54	1.viii.54	1	8.ix.54
		2.viii.54	2	
		8.viii.54	1	
		9.viii.54	1	
		10.viii.54	2	
		28.viii.54	1	

* One of these larvae pupated 9.viii.54.

Within hours of samples being taken from the band of turgid eggs, rain filled the tank to capacity and the band remained submerged for weeks. Thirty-four days after submergence, examination of this band showed that many eggs had hatched, but, from a sample taken, eggs continued to hatch during the succeeding 5 days.

During the 34-day interval two additional bands had been deposited—one near the rim of the tank was dry and the eggs collapsed, while the other was in the capillary strip and comprised turgid eggs. Samples from this band were stored on moist paper in an air-tight tin at room temperatures. On five occasions during the ensuing 5 months portions of this sample were immersed in water and hatching observed. Details of the hatching of the last two samples are given in Table 3 and provide evidence of decidedly irregular hatching times following immersion.

TABLE 4
MOSQUITO SPECIES ASSOCIATION WITH LARVAL HABITATS

Habitat	Species	Remarks
Open concrete or iron water-storage tanks	<i>A. queenslandis</i> always found, <i>An. annulipes</i> very occasionally	Permanent habitats, very limited in number, contributing only a small maintenance population
Domestic tanks and discarded motor tyres	<i>A. notoscriptus</i> occasionally	Permanent habitats
Wells or small grassy water-holes	<i>An. annulipes</i> frequently found, also <i>C. p. australicus</i> at times and occasionally <i>A. alboannulatus</i>	These habitats do not breed continuously; their suitability may depend on rising level inundating marginal grass
Earth tanks (stock watering dams)	<i>C. p. australicus</i> probably the most common species, then <i>An. annulipes</i> . (<i>C. fatigans</i> in a heavily polluted dam)	The conditions of the margins were most important in determining whether or not breeding occurred in these habitats and, although permanent, larval populations were erratic
Permanent grassy pools in creeks not normally flowing	Limited <i>An. stigmaticus</i> usually recorded, <i>An. annulipes</i> variably present	Only low populations were recorded in these situations which were very limited in occurrence
Temporary grassy pools in creeks, usually excavated below a drop, with overhanging grasses	<i>An. annulipes</i> , <i>A. stigmaticus</i> , <i>C. p. australicus</i> could all be found, and at times <i>A. alboannulatus</i> in the more exposed of these habitats	One small creek in which such holes predominated invariably had <i>An. stigmaticus</i> when water was present
Marginal vegetation of large pools in gently flowing stream (Stockyard Creek)	<i>An. annulipes</i> commonly, <i>An. stigmaticus</i> fairly frequently. <i>C. pseudomelanoconia</i> at times common, and <i>C. fergusonii</i> occasionally	A permanent breeding habitat of variable seasonal significance but never in any sense an intense breeding ground
Small rock-pools with intense leaf pollution	Always <i>A. notoscriptus</i> with some <i>A. queenslandis</i> at times	Some such pools had a high degree of permanence and maintained continuous populations of <i>A. notoscriptus</i>
Rock-pools with moderate leaf pollution, in sheltered situations	<i>A. queenslandis</i> always present <i>A. notoscriptus</i> , <i>An. annulipes</i> , and <i>An. stigmaticus</i> sometimes recorded	In sheltered situations, on a rocky catchment these pools were virtually permanent and maintained continuous populations of <i>A. queenslandis</i>
Rock-pools, with some leaf pollution in exposed situations	<i>A. alboannulatus</i> commonly found, but <i>A. queenslandis</i> and <i>A. notoscriptus</i> also likely to be recorded	These pools were only temporary in nature but could be maintained for periods by suitably spaced falls of rain. When present they probably made a significant contribution to the overall population

TABLE 4 (Continued)

Habitat	Species	Remarks
Temporary pools in incipient gullies either in earth or part earth, part rock	<i>A. alboannulatus</i> in high populations. <i>A. queenslandis</i> rare, and <i>An. annulipes</i> and <i>C. p. australicus</i> sometimes present	Shortly after forming, these pools almost invariably presented high populations of <i>A. alboannulatus</i> larvae
Temporary water-holding depressions of moderate size in open grassland	<i>A. alboannulatus</i> may occur in high populations	A very limited type of breeding habitat unusual in this area
Hoof-prints in seepage areas	<i>An. annulipes</i> commonly; <i>C. annulirostris</i> and <i>C. p. australicus</i> have also been taken	The more typical grassy bogs in this area appear to be innocent of mosquito breeding
Jars of water suspended in trees	<i>A. notoscriptus</i> most commonly with <i>Tripteroides</i> sp. on one occasion	Jars of water were placed in tins nailed to tree trunks to simulate tree-holes
Water-tank of seldom used steam engine	Permanent breeding of <i>A. notoscriptus</i> , with <i>Tripteroides</i> sp. rarely	The contained water was a particularly strong leaf infusion

These observations suggest that eggs of *A. queenslandis* are normally deposited on moist granular surfaces. They are apparently unable to withstand air drying and therefore hatching depends on a frequently fluctuating water level. Rocky Creek, with its spring-fed, semi-permanent rock-pools often refreshed by rain, provides ideal conditions. It is significant that adults of this species have been collected at site 8 in this creek during each month of the year. It is not known whether its eggs are able to withstand repeated immersions but this is probable.

Provided the eggs are maintained in a moist condition, but are not actually immersed in water, they can remain viable for at least 5 months. Once immersed, the hatching times of the eggs have proved to be quite irregular and a proportion of viable eggs may remain unhatched for at least 5 weeks. The factors governing this retardation of hatching are not known but obviously they could have an important bearing on the survival of the species. Spacing of adult emergence over a protracted period could be important where short-term exigencies such as unfavourable weather or absence of hosts need bridging. The effect of flushing of larvae from breeding holes by torrential rains can be amended by the presence of a residue of unhatched eggs.

As indicated below, recently formed temporary pools in incipient gullies invariably present high populations of *A. alboannulatus* larvae. These must have hatched from eggs already present within the dried water-hole prior to the filling and it is suggested that this species oviposits at the margins of receding temporary pools.

A capacity for delayed hatching, if possessed by *A. alboannulatus*, could very effectively protect this species from complete extinction from any one breeding place in the event of inadequate run-off after rains. It has been frequently observed that pools formed under such circumstances do not persist long enough to allow larvae to mature. This capacity then would ensure that a residue of viable eggs remains ready to take opportunity of later rains.

(b) *Larvae*

Observations on larval distribution were undertaken early in the study, overlooked during our preoccupation with virus recovery, then given further attention in the spring of 1953 and at least at monthly intervals to the end of July 1954.

The associations of species with larval habitats are detailed in Table 4. The more general conclusions resulting from these periodic surveys are as follows:

- (i) Although some were not taken on all occasions when larval sampling was undertaken, five species, namely *Anopheles annulipes* and *Ae. stimulans*, *Aedes alboannulatus*, *A. queenslandis*, and *A. notoscriptus* were always present even though their abundance fluctuated.
- (ii) Most of the species of *Culex* recorded from the area were decidedly limited in their seasonal occurrence.
- (iii) The most important species complex with different habitats concerned *A. queenslandis* and *A. alboannulatus*. Of these *A. queenslandis* was persistently present in its typical rock-hole breeding grounds, many of which under average conditions are virtually permanent breeding places. *A. alboannulatus*, on the other hand, characteristically populated the rather ephemeral earth-bound pools appearing after rain in juvenile gullies and small depressions on the slopes. Nevertheless, the characteristic habitats of each could sometimes be found in the one pool and both species could occur.
- (iv) It is believed that the larval populations of both *A. queenslandis* and *A. alboannulatus* are independent of immediately pre-existing adult populations since eggs are obviously present in quite large numbers in potential breeding habitats.
- (v) For the dominant species of the area, except perhaps *A. alboannulatus*, it was obvious that both permanent and temporary breeding grounds existed. The degree to which the permanent habitat contributed to the maintenance of a noticeable level of adult population differed considerably with the species: they were of little value in the case of *Ae. annulipes* and *C. annulirostris*, but of considerable value for *A. queenslandis* and *A. notoscriptus*.
- (vi) Although it will be seen (Table 4) that a wide variety of larval habitats were available over the area, these were limited in both number and extent. High larval populations could be, and were, recorded for individual pools and even for the majority of available pools, but the physical limitations were such that really high adult populations could never be recorded.
- (vii) Some species occasionally taken as adults have not been found in larval surveys. Apart from the possibility of tree-holes which are difficult to locate, we do not think that we have overlooked any particular larval habitats and our failure to record larvae of species such as *Theobaldia inconspicua* and *Culex postspiracularis* is probably due to their very low incidence.

(c) *Adults*

(i) *Seasonal Abundance*.—The Mt. Flora area is one in which the adult mosquito population is not obvious. The casual observer moving through the area would seldom be attacked by mosquitoes and never by numbers likely to cause even a slight degree of annoyance. It is only when the observer is more or less stationary for periods of

TABLE 5
NUMBERS OF MOSQUITOES ATTRACTED TO HUMAN BAIT AT VARIOUS TIMES OF THE YEAR
Figures in brackets indicate number of collections made on each day

Date	Morning Collections (ranging)	Morning Collections (Rocky Creek)	Afternoon Collections (Rocky Creek)	Evening Collections (ridges)	Totals when Two or more Collections Made on One Day
18. ii. 53	73	—	72	12	157 (3)
19. ii. 53	23	—	—	50	73 (2)
9. iii. 53	—	—	*	*	44 (2)
10. iii. 53	†	—	†	†	83 (3)
11. iii. 53	—	—	116	9	125 (2)
12. iii. 53	—	—	122	16	138 (2)
14. iv. 53	—	—	140	6	146 (2)
15. iv. 53	8	—	126	34	168 (3)
16. iv. 53	13	—	120	36	169 (3)
17. iv. 53	42	—	—	—	—
16. xi. 53	—	—	—	23	—
17. xi. 53	—	68	35	9	112 (3)
18. xi. 53	—	16	—	46	62 (2)
19. xi. 53	—	—	—	22	—
20. xi. 53	—	103	—	—	—
21. xi. 53	6	—	—	13	19 (2)
22. xi. 53	—	47	—	10	57 (2)
23. xi. 53	13	—	—	—	—
24. xi. 53	2	—	—	3	5 (2)
17. ii. 54	—	—	9	8	17 (2)
18. ii. 54	2	—	11	9	22 (3)
19. ii. 54	Nil	34	—	8	42 (3)
20. ii. 54	—	—	—	5	—
23. iii. 54	—	—	5	11	16 (2)
24. iii. 54	—	16	—	47	63 (2)
25. iii. 54	13	—	—	38	51 (2)
22. iv. 54	—	—	—	29	—
23. iv. 54	—	29	—	6	35 (2)
24. iv. 54	—	43	—	15	58 (2)
25. iv. 54	—	45	36	11	92 (3)
28. iv. 54	—	18	—	6	24 (2)

TABLE 5 (Continued)

Date	Morning Collections (ranging)	Morning Collections (Rocky Creek)	Afternoon Collections (Rocky Creek)	Evening Collections (ridges)	Totals when Two or more Collections Made on One Day
31.v.54	—	—	134	1	135 (2)
1.vi.54	—	36	—	5	41 (2)
2.vi.54	5	9	—	Nil	14 (3)
28.vi.54	—	—	—	Nil	
29.vi.54	—	12	85	3	100 (3)
30.vi.54	—	—	147	—	
Average per collection site	16.6	37.4	82.7	19.4	39.1

* Afternoon and evening collections not differentiated.

† Morning, afternoon, and evening collections not differentiated.

ten minutes or more that an appreciable attack is noticed. Hence observation techniques became fairly standard and it is possible to tabulate the total mosquito collections made in three ecological areas and at three different periods of the day these places and times being virtually the same for all collections.

Table 5 summarizes all such comparable catches made at intervals over the period February 1953 to the end of June 1954. Although numbers fluctuated, no marked seasonal influence on general adult abundance is shown. Daytime catches do reflect variations in adult populations but these are not evident in collected. The day-to-day climatic variations are of more importance in determining the size of particular catches, although seasonal climatic influences are responsible for diminished evening activity during winter. Later observations have also shown that prolonged periods of excessive rainfall may give rise to higher levels of population than are recorded here. On such occasions the species derived from permanent breeding habitats are partially suppressed and those derived from temporary habitats assume dominance.

Table 5 suggests that a definite mosquito season does not occur during the warmer months of the year. On the contrary, winter populations can be quite as high as average summer populations.

Biting Activity.—Observations of biting activity covered all periods of the day from 0845 to 2000 hr. and it was found that mosquitoes were likely to attack at any time within this period. A later observation by Myers indicates that early morning activity does occur at least in the Flaxing (best) area during summer. Evening collections were continued up to 9 hr after cessation of activity and in the main this occasion was complete. It is still possible that species such as *A. annulipes* may be active in a later period. Under exceptional conditions observed subsequently, when night

temperature and humidity were unusually high, spontaneous attack by *A. vigilax* and *C. annulirostris* was observed up to 2200 hr (February 9, 1955, at site 1).

Within the period 0845–2000 hr two types of activity were distinguished. The first, experienced during the daytime, was stimulated by the presentation of a blood source within suitable diurnal resting zones. This activity could be intense (by the standards of this particular area) when resting zones approximated important larval habitats, but was still quite noticeable in sheltered patches of scrubby vegetation (*Styppandra glauca* and *Olearia viscidula*) or paper-bark thickets on slopes well away from breeding grounds. In the vicinity of breeding grounds lacking adequate adult shelter, however, diurnal attacks were not experienced except for an odd mosquito or two.

The second type of activity was experienced during the early evening. Although collections were concentrated on two particular ridges (sites 2 and 7), certain other areas were included from time to time (sites 13, 14, 16, 19, and 20); on almost all occasions it was obvious that a wave of attack took place some time during this evening period. And it was obvious from the type of attack that the mosquitoes were ranging in search of their blood feeds.

Daytime collections at stations away from major *Aedes* breeding habitats were self-terminating and, in the main, the available population likely to be attracted to man was caught within the first half hour in the particular spot being exploited. An exception to this was found in the Rocky Creek area where attack could commence almost immediately following bait exposure and, if so, catches were likely to be high. The catches in this area were not self-terminating but appeared to be strongly correlated with hour by hour meteorological conditions.

In this Rocky Creek area, three distinct phenomena were observed. The first occurred during morning catches and concerned an abrupt reduction in attack rate at about 1000 hr. This occurred on a number of occasions and appeared to be related to the entry of appreciable sunlight beneath this canopy.

The other phenomena concerned the type of attack which might be experienced at any time during daylight. There were times when the catches made seemed to comprise genuinely hungry mosquitoes; on other occasions, even though the catch made might be considerable, the relative indifference to blood feeding, as well as the observations of collectors in their immediate vicinities, led to the belief that a moving population was being intercepted. Of these two types of catches the latter seemed to predominate.

Catches within the evening activity period varied considerably but usually when observations were made a limited period of intensified activity was apparent even when low catches were recorded. The time at which the intensification occurred was always within the hour following the setting of the sun behind the western escarpment and, consequently, was latest in midsummer and earliest in midwinter.

The periods of intensified feeding activity at dusk could not be correlated with temperature or humidity within the limits registered. Nor did the obscuring of the sun by heavy cloud banks in the west appear to occasion an earlier onset. However, the flush periods of activity can be lengthened when cloudy conditions are combined

TABLE 6
EVENING ACTIVITY PERIODS

Date	Sun-set (hr)	Peak Activity (hr)	Temperature at Peak of Activity Period (°F)	Relative Humidity at Peak	Catch (No. of collectors in brackets)	Other Conditions
16.xi.53	1830	1850-1920	66	73	23 (5)	Rocky Creek attack terminated 1950
17.xi.53	1831	1915-1945	82	59	9 (5)	
18.xi.53	1832	1900-1910	76	70	46 (5)	
19.xi.53	1833	1800-1930	63	94	22 (5)	
21.xi.53	1834	1857-1930			13 (3)	
22.xi.53	1835	Not recorded			10 (3)	
24.xi.53	1837	1900-1930	55	67	3 (4)	
17.ii.54	1839	1915-1940	69	85	8 (3)	
18.ii.54	1838	1915-1930			9 (4)	
19.ii.54	1837	1900-1935			8 (3)	
20.ii.54	1837	1907-1930			5 (4)	
23.iii.54	1745	1750-1838	68	40	11 (2)	Convection not well defined
24.iii.54	1744	1755-1845	64	55	47 (2)	Excellent convection, ceased about 1840 hr
25.iii.54	1743	1756-1847	69	41	38 (2)	Excellent convection, over by 1850 hr
22.iv.54	1718	1735-1810	64	80	29 (3)	Of this total 22 were from an evening catch in Rocky Creek
23.iv.54	1717	1735-1810	64	85	6 (2)	
24.iv.54	1716	1740-1830			15 (4)	
25.iv.54	1715	1730-1800			11 (5)	
28.iv.54	1712	1720-1815			27 (4)	
						21 of this total from Rocky Creek
31.v.54	1648	1715			1 (2)	
1.vi.54	1648	1705-1740			5 (2)	
2.vi.54	1648	No activity			Nil (2)	
28.vi.54	1649	No activity			Nil (4)	
29.vi.54	1649	Approx. 1700			3 (4)	

with high relative humidity. The sudden increase in attack rate occurred before darkness set in but may well have been triggered-off by a reduction in light values to a very low threshold.

Nevertheless, day-to-day variations required some other explanation and we gradually came to correlate high catches with calm evenings following sunny days, when a gentle convection draught could be detected moving steadily up the slopes.

For the period February to April 1953, of seven evenings for which detailed records were kept, there were three when catches on the ridges exceeded 30 for the evening biting periods. These were the flushes of activity which it was thought correlated with convectional air movement (see Table 6). An attempt to repeat these observations in 1954 met with little success until March 24 and 25 when high catching rates were again associated with obvious convection currents.

In confirmation of this association it should be noted that on the previous evening March 23, 1954 a low catch was recorded although conditions of temperature and humidity were similar. On this occasion, gusty winds prevented the development of the convection flow but it was not sufficiently turbulent to completely suppress feeding activity. On two or three other occasions, when part of the collecting team was exposed on grassy slopes, winds strong enough to prevent actual attack were experienced. These winds did not, however, prevent movement as mosquitoes were seen and heard. Again, on quite calm evenings when, for reasons not yet understood, the convection flow did not develop, collections were larger than on turbulent nights. However, they were never as large as those made on calm evenings when the convection flow was detectable.

In Rocky Creek (site 8), where daytime attack rates were considerably higher than elsewhere, there was also a cessation of activity after the evening biting period. As an example of this may be quoted the catches made by two collectors on November 23, 1953. For the period 1752-1807 hr, 39 mosquitoes were recovered, from 1823 to 1853 hr the catch was 17, and from 1853 to 1945 hr only four were caught. A similar cessation was experienced on other occasions and since this area was in the immediate vicinity of important breeding habitats we consider the phenomenon of cessation elsewhere observed to be a true cessation and not an exhaustion of mosquitoes present in the vicinity of the collectors.

Catching rates, as such, were not seriously investigated, but on a number of occasions catching was indulged in for periods of 30, or more frequently, 60 min. For the sake of comparison with other regions, and incidentally to give an indication of the population level, catches per man per hour are recorded in Table 7 for Rocky Creek, the most productive of our catching stations. These are more or less random samples for neither the highest nor the lowest catches were recorded in this way.

Although catching rates varied from day to day, it was also obvious that the selection of position by the collector was quite important. On June 30, 1954, three collectors were deliberately spaced at intervals approximating 100 ft up the creek (site 8), and the individual recoveries were 58, 76, and 13 for the period 1515-1615 hr, giving the average of 49 recorded in Table 7.

No mosquito activity was detected on the tops of the hills and little on the saddles connecting them. On the lee side of these saddles evening activity was observed quite close to their crests. However, in these zones observations were most inconclusive as strong winds prevailed on the occasions when these environments

were investigated. Nevertheless, definite breeding habitats were present on the saddles, and though it may be presumed that local blood feeding takes place, conditions conducive to this activity were not observed.

The steep slopes below these saddles are predominantly exposed to the west and south-west and are largely devoid of breeding habitats. This environment was not considered worth serious investigation. Here and there sheltered gullies run from the lower breeding ground level almost to the top ridge level. In these there has been evening mosquito activity at sufficiently varying levels to indicate a general dispersal of adult mosquitoes.

On the lower timbered ridges between the creeks where these have become patent breeding grounds, and for some distance above, evening mosquito activity has almost always been observed. This activity had all the appearance of being generalized, whereas, in the daytime, although catches could be made from time to time, much seemed to depend on the spot selected. No daytime catches were made in exposed situations but areas with light canopy shade reinforced by ground vegetation of about 4 ft (*Stypandra glauca*) were generally productive.

TABLE 7
CATCHING RATES AT SITE 8, EXPRESSED AS MOSQUITOES PER MAN PER HOUR

Date	Morning	Afternoon	Evening
22.xi.53	27		
23.xi.53			49
19.ii.54	14		
23.iv.54	15		
24.iv.54	37		
25.iv.54	45	6	
28.iv.54	9		21
29.vi.54	7	61	
30.vi.54		49	

The most important habitat differences were found in the various creeks of which Stockyard Creek and Rocky Creek were the two extremes. Both are permanent larval habitats. The former predominantly breeds *Anopheles* spp. and at times *Culex* spp. including *C. pipiens australis*, but *Aedes* spp. are not completely absent. The latter is predominantly an *Aedes* area but *Anopheles* spp. also occur as larvae. Very little adult activity has been observed in Stockyard Creek, indicating that it is not a complete habitat for all types of mosquito activity. Rocky Creek displays adult activity at almost all times and is apparently a permanent and complete habitat, providing suitable conditions for breeding, feeding, and resting.

(iii) *Resting Places*.—Resting places characteristic of other areas, especially in riverine environments, such as hollow logs and tree stumps, were uncommon and, like rabbit warrens, were unproductive at Mt. Flora. On the other hand, abundant opportunities existed for resting in rock crevices and low vegetation and it was in such places that resting was eventually disclosed. Nevertheless, recoveries of resting adults for some species remain very meagre and for these a characteristic resting habitat has yet to be discovered.

Table 8 records resting place recoveries which were fully analysed for species and habitats. The catches recorded in Table 14 attain a higher total. Those in excess of the numbers recorded in Table 8 were not differentiated for the particular type of resting habitat.

High proportions of males in the catches are of course indicative of proximity of breeding grounds and this is true of *An. stigmaticus*, *A. queenslandis*, and *C. pipiens australicus*. On the other hand, only female *A. notoscriptus* were taken even though known breeding habitats were close by, and the circumstances of collection indicated that these were being attracted to the collector. *C. annulirostris* also was represented by females only, but the breeding habitat was in all probability distant from the point of collection and true resting was being observed. The sex ratios of the catches of *A. alboannulatus* and *A. queenslandis* are in line with the known larval habitat distribution of these species.

TABLE 8
ANALYSIS OF RESTING PLACE CATCHES

Species	Grasses		Herring-bone Fern		Rock Crevices		Debris		Hollow Logs		Warrens		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<i>Anopheles stigmaticus</i>		1		1	3	5	7	6					10	13
<i>An. annulipes</i>		2							1		1		1	3
<i>Aedes alboannulatus</i>	1	8		4	6	18							7	30
<i>A. queenslandis</i>	1	2	12	19	85	98							98	119
<i>A. notoscriptus</i>				5		6								11
<i>A. rubrithorax</i>				1										1
<i>Culex pipiens australicus</i>			5	22	16	11					5	9	26	42
<i>C. annulirostris</i>				15		7								22
<i>C. fergusonii</i>		1												1
<i>C. pseudomelanoconia</i>						1								1
<i>C. postspiraculosus</i>				1										1

Resting habitat catches are further analysed in Table 9 for the condition of the wing fringe (a rough indication of age) and of the female abdomen.

It will be seen that catches generally comprised fairly fresh individuals. Little information on the resting of females digesting a blood meal was gleaned except in the case of *An. stigmaticus* for which a significant percentage of blood-engorged individuals was recorded. Again, gravid females were seldom taken, except in the case of *C. pipiens australicus*.

Of the resting habitats from which adult mosquitoes were taken the most successful were rock crevices which abounded in some of the creeks of the area. It was difficult to distinguish between resting in actual rock crevices and in the leaf and stick debris so frequently associated with the crevices in dry parts of the creeks. Strictly, in the areas where most recoveries were made, boulders and debris were ubiquitous, and appeared to provide a stable resting habitat. Somewhat different was the herring-bone fern habitat which, at the same spot, gave good recoveries at times and almost nothing on other occasions.

Finally, although the results recorded for *An. stigmaticus* are low, these are not complete. Collecting in rock crevices, debris, and under fallen logs beside breeding habitats can yield a significant recovery of blood-engorged specimens.

(iv) *Blood Sources* (see Tables 10 and 11). The much exploited technique of allowing mosquitoes to be attracted to man naturally revealed quite a range of species willing to take a blood feed from this host. Such information was of little importance since man is not a normally available blood source in the areas investigated. Some further information was gained by watching animals (rabbit and dog) exposed in bait traps. By far the most illuminating information was gained from precipitin testing of engorged females taken in resting habitats, and particularly those attracted to human bait.

TABLE 9
CONDITION OF SPECIMENS CAUGHT RESTING

Species	Habitat	Wing Fringe*		Abdomen†
		♂	♀	♀
<i>Anopheles stigmaticus</i>	Herringbone fern	—	0 : 1 : 0 : 0	0 : 0 : 1
	Rock crevices and debris	1 : 2 : 0 : 0	1 : 3 : 1 : 0	3 : 0 : 2
	Debris	4 : 2 : 1 : 0	2 : 4 : 0 : 0	3 : 0 : 3
<i>Aedes alboannulatus</i>	Herringbone fern	—	2 : 0 : 2 : 0	0 : 0 : 4
	Rock crevices and debris	1 : 5 : 0 : 0	7 : 9 : 3 : 0	1 : 0 : 18
	Grasses	0 : 1 : 0 : 0	7 : 0 : 0 : 0	0 : 0 : 7
<i>A. queenslandis</i>	Herringbone fern	4 : 7 : 1 : 0	8 : 9 : 1 : 0	3 : 0 : 15
	Rock crevices and debris	24 : 52 : 9 : 0	29 : 63 : 11 : 0	2 : 1 : 101
	Grasses	1 : 0 : 0 : 0	1 : 0 : 1 : 0	—
<i>Culex annulirostris</i>	Herringbone fern	—	4 : 16 : 0 : 0	0 : 0 : 20
	Rock crevices and debris	—	2 : 5 : 0 : 0	0 : 0 : 7
<i>C. pipiens australicus</i>	Herringbone fern	1 : 4 : 0 : 0	9 : 13 : 0 : 0	2 : 5 : 16
	Rock crevices and debris	2 : 11 : 3 : 0	3 : 8 : 0 : 0	0 : 2 : 9
	Warrens	4 : 1 : 0 : 0	4 : 5 : 0 : 0	0 : 4 : 5

* Wing fringe ratio—numbers of individuals with wing fringe intact: slightly damaged: badly damaged: denuded.

† Abdomen ratio—number of individuals with abdomen blood-distended: gravid: undistended.

Some recovery of engorged specimens has resulted from evening ridge collections (sites 2 and 7) but in the main these have been positive for man, indicating unobserved feeding on the collecting party; nevertheless, a few have been significant. Most productive has been the Rocky Creek habitat (site 8) where important information as to rabbit and marsupial feeding has been obtained.

For the collections made between November 1953 and July 1954, 946 mosquitoes attracted to man in Rocky Creek were collected. Of these 112 or 11·8 per cent. were

TABLE 10

OBSERVED BLOOD FEEDING AND RESULTS OF PRECIPITIN TESTS*

+, feeding observed; numbers in brackets represent positive precipitin tests

Species	Blood Source						
	Man	Rabbit	Marsupial	Ox	Horse	Dog	Fowl
CULICIDAE							
<i>Anopheles stigmaticus</i>			(3)				
<i>An. annulipes</i>	+	(12)	(4)				
<i>Tripteroides atripes</i>	+						
<i>Tripteroides</i> sp.		(1)					
<i>Taeniorhynchus linealis</i>	+	(3)					
<i>Aedes notoscriptus</i>	+	(134)	+	(25)			
<i>A. alboannulatus</i>	+	(154)	+	(20)			
<i>A. queenslandis</i>	+	(96)	+	(40)			
<i>A. biocellatus</i>	+						
<i>A. subauridorsum</i>	+	(1)					
<i>A. rubrithorax</i>	+	(37)					
<i>A. vigilax</i>	+	(21)	+	(2)			
<i>A. vittiger</i>	+						
<i>Culex annulirostris</i>	+	(7)					
<i>C. fatigans</i>		(1)					
<i>C. pipiens australicus</i>		(2)					
SIMULIIDAE		(3)					
<i>Austrosimulium furiosum</i>	+						
<i>A. bancrofti</i>	+						
CERATOPOGONIDAE							
<i>Leptoconops stygius</i>	+	(4)	+	(6)			
<i>Lasiohelea townsvillensis</i>	+		+	(3)			
<i>Culicoides magnimaculatus</i>	+	(48)					
<i>C. parvimaculatus</i>	+	(1)					
<i>C. bancrofti</i>	+						
<i>C. antennalis</i>	+	(2)					
<i>C. marksi</i>	+						
<i>C. dycei</i>	+						
<i>C. nattaiensis</i>		(1)					
TABANIDAE							
<i>Dasybasis circumdata</i>							
<i>D. circumdata</i> (dark form)	+						
<i>D. indefinita</i>	+						
<i>D. neobasalis</i>							
<i>D. gentilis</i>							
<i>D. innotata</i>	+						
<i>D. oculata</i>	+						
<i>Scaptia xanthophilis</i>	+						
<i>S. auriflua</i>	+						
<i>Cydistomyia</i> spp.							
(2 undescribed species)	+	+					

* In interpreting this table, it should be remembered that most of the observations and most of the material used for precipitin tests resulted from insects attracted to man. In the case of our preparations for precipitin tests, although we tried to avoid smearing the mosquitoes known to have fed on the collector, in the case of any doubt, test smears were prepared and there is, inevitably, an unnatural bias towards man.

smearcd for precipitin tests and 50 or 5.3 per cent. gave positive reactions for man, 44 or 4.6 per cent. were positive for either rabbit or possum, and 18 or 1.9 per cent. were negative. Thus, over a long period, this particular method yielded 4.6 per cent. of

TABLE 11
SOURCE OF BLOOD-FED MATERIAL FOR PRECIPITIN TESTS*

Species and Host	Attracted to Man in Creeks	Attracted to Man on Ridges	Natural Shelters	Rabbit Bait	Light-trap
<i>Aedes alboannulatus</i>					
Man +	10	132	1		1
Possum +	8	2			
Rabbit +	2	5		10	
Negative	3	4			
<i>A. queenslandis</i>					
Man +	45	32	1		
Possum +	46	4	1		
Rabbit +	17	1		13	
Negative	31	2	1		
<i>A. notoscriptus</i>					
Man +	15	114	1	1	
Possum +	2	5		1	
Rabbit +				14	
Negative	1	8		2	
<i>A. rubrithorax</i>					
Man +	1	35		1	
Possum +	1	5			
Rabbit +		4		1	
Negative		3			
<i>A. vigilax</i>					
Man +		17		1	
Rabbit +	1				
Negative		1		1	
<i>Anopheles stigmaticus</i>					
Possum +			3		
Negative			7	1	
<i>An. annulipes</i>					
Man +		22			
Possum +		4			
Rabbit +		12		2	
Negative		7			
Totals	183	419	15	48	1
Totals (excluding positives for man and negatives)	77	43	4	42	—

* Values in this table do not coincide with those of Table 10 because the habitat from which specimens were collected for precipitin tests was not always recorded.

engorged specimens prepared to investigate the possibility of a further blood meal. In collections from shelters only four significant positives (i.e. for hosts other than man) were recorded from some 450 mosquitoes or approximately 1 per cent.

At one stage it was considered that collections from Rocky Creek might be unnecessary for virus-recovery work owing to the proximity of breeding habitats and the probability of most catches being recently emerged. The continued catching rate in this area was a partial negation of this premise, but of greater significance was the recovery of recently fed specimens (6.5 per cent. when negative precipitin tests are included since these are usually blood feeds in which digestion has proceeded too far for a reaction to be recorded).

Most of the results for precipitin tests were obtained when the rabbit population was decidedly reduced, and although we had no means of gauging the extent of the marsupial population, it is most unlikely that they were unusually numerous for a relatively virgin area, but considerably more abundant than in many other rabbitry regions. Marsupials appear to be the common natural blood source for *A. albomaculatus*.

TABLE 12
COMPARATIVE YIELDS OF BLOOD-SUCKING INSECTS FROM RABBIT AND HUMAN
BAITS AT SITE S

Total period of baiting = 9.3 hr

Species	Rabbit Yield	Human Yield
<i>Aedes queenslandicus</i>	18	48
<i>A. albomaculatus</i>	5	19
<i>A. notoscriptus</i>	4	5
<i>A. vigilax</i>	1	3
<i>Culex annulirostris</i>	1	—
<i>Lasiocheilus townsendi</i>	2	—
<i>Culicoides magnimaculatus</i>	—	1
Total yields	31	76

and *A. queenslandicus*, and the rabbit also serves significantly for both *A. notoscriptus*, *A. annulipes*, and *A. signatus* attack marsupials but in the case of the first two rabbits are also attacked. Rabbit feeding by *A. annulipes* and *C. pipiens australicus*, although confirmed in this area, is obviously not of the importance attained in some areas west of the Dividing Range.

Finally the results of limited trials of animal-baited drop traps still deserve some mention. The type used was that of Myers (1956) and the bait was usually rabbit but dog and possum were also tried.

The animal bait was exposed for standard intervals of 15 min with a human control approximately 20 ft away from the trap. The comparative catches obtained for rabbit and human bait are recorded in Table 12. Engorged specimens from these trappings were smeared for precipitin tests.

c. Distribution in Various Habitats and at Different Times of the Year.—Table 13 presents an analysis of the catches made from the various habitats which were repeatedly investigated at different times of the day. The information presented therein has particular reference to individual species differences and these are discussed in the following section.

Similarly, such seasonal variations as were detected are shown in Table 14 and their importance is discussed in the following section.

(d) *Individual Species*

In this section reference should be made to Tables 4, 8, 10, 13, and 14 for substantiation of many of the statements made.

TABLE 13
HABITAT DISTRIBUTION OF MOSQUITO SPECIES

Species	Resting in Natural Shelters	Attracted to Man					Totals
		Morning		After- noon	Evening		
		Rocky Creek	Ridges	Rocky Creek	Ridges	Rocky Creek	
<i>Anopheles stigmaticus</i>	34				1		35
<i>An. annulipes</i>	4				56		60
<i>Aedes alboannulatus</i>	56	50	10	29	60	54	259
<i>A. queenslandis</i>	312	332	9	394	58	174	1279
<i>A. alboannulatus</i>	}		109	584	92		785
<i>A. queenslandis</i>							
<i>A. notoscriptus</i>	16	26	37	40	105	7	231
<i>A. quasirubithorax</i>					1		1
<i>A. subauridorsum</i>		3					3
<i>A. biocellatus</i>		4					4
<i>A. rubrithorax</i>	1	1				1	3
<i>A. vigilax</i>			1	1	4		6
<i>A. vittiger</i>					1		1
<i>Culex annulirostris</i>	28	8	12	18	57	1	124
<i>C. pipiens australicus</i>	69						69
<i>C. pseudomelanoconia</i>	1						1
<i>C. fergusoni</i>	1						1
<i>C. postspiraculosus</i>	1						1
<i>Theobaldia inconspicua</i>	3						3
<i>Uranotaenia pygmaea</i>	1						1
<i>Tripteroides atripes</i>		2	2	2			6
<i>Taeniorhynchus linealis</i>					3		3

* These species were undifferentiated.

(i) *Anopheles stigmaticus*.—Larvae of this species were found at least throughout the cooler part of the year from April to August though it may or may not be present during the summer. Adult collections suggest that it is likely to be present at most times of the year since failure to record it usually meant that suitable resting places were not investigated. Frequently associated with *An. annulipes*, it was found breeding in a variety of situations in most creeks except the exposed temporary rock-holes. Its larvae are usually associated with the margins of large pools with

overhanging banks, mostly pools in earth, but sometimes in rock-pools with some vegetation or algae, and often sheltering below a rock overhang.

Adults have not usually been taken except in the vicinity of breeding areas and are not attracted to animal bait (one was collected in a tent trap baited with rabbit, one or two others were attracted to man but did not bite). It is now known that blood-engorged females may be obtained fairly easily in resting places, usually on piles of flood debris. The high ratio of negative precipitin tests is regarded as significant for this species. So far possum (or some other marsupial) is the only known natural blood source but since wombat blood does not record a positive with our anti-possum serum the possibility of wombat feeding remains; or again some entirely different blood source may be utilized. Whatever it is we would expect it to be found in the immediate environment of the creek breeding areas.

TABLE 14
MOSQUITO CATCHES AT DIFFERENT TIMES OF THE YEAR

Species	1953				1954				
	Feb.	Mar.	Apr.	Nov.	Feb.	Mar.	Apr.	May-June	June
<i>Anopheles stigmaticus</i>	7	2		4			20		
<i>An. annulipes</i>	16	12	5	9	5	7	15	2	
<i>Aedes alboannulatus</i>				224	14	22		1	1
<i>A. queenslandis</i>				560	31	37	258	181	239
<i>A. alboannulatus</i>									
<i>A. queenslandis</i> } *	157	250	467						
<i>A. notoscriptus</i>	23	51	40	48	11	56	42	7	4
<i>A. vigilax</i>	1	2			2	1			
<i>Culex annulirostris</i>	3	7	53		11	30	30		
<i>C. pipiens australicus</i>	1	2		31		17	20		

* These species were undifferentiated.

For our present purposes this species is of no practical importance, though it is of considerable academic interest that its blood-feeding habits should eventually be disclosed.

(ii) *Anopheles atratipes*.—A single female of this species was collected from human bait during April 1956.

(iii) *Anopheles annulipes*.—Rather more widely distributed than *An. stigmaticus* and occurring throughout the year this species exploits the same breeding habitats but is also found in growths of *Spiraea* and more frequently in marginal grassy paddies to the streams and in the longer-lasting grassy temporary pools.

Although taken biting man on one occasion in the daytime it is, as elsewhere, typically an evening biter. During the evening activity period, onset of biting by *An. annulipes* commenced later than with the species of *Aedes*.

The rather uniform catches of adults of this species recorded throughout the year suggest that it does not attain any appreciable seasonal peak. Almost the entire catch resulted from evening activity on the ridges which is highly suggestive of pronounced ranging.

Typical diurnal resting places were not found and rabbit warrens and hollow stumps were not utilized in the characteristic fashion of inland areas. There may be other typical resting places, but it seems more likely that the diversity of possibilities of resting in vegetation at Mt. Flora is such that there is no concentration of resting.

(iv) *Tripteroides sciripes* and *Tripteroides* sp.—Although recorded in limited numbers *T. sciripes* occurred fairly widely over the area and was usually collected attacking man, commonly on the tip of the nose. Larvae were recovered from an engine tank and a glass jar attached to a tree trunk. Another species of *Tripteroides* was also represented in this latter habitat.

(v) *Uranotaenia pygmaea*.—This typically tropical genus does extend its range well to the south with the one species *U. pygmaea*. All previous records south of Queensland have been, as far as we are aware, strictly coastal, so the present record of this species is unusual. It was taken resting at Stockyard Creek, site 3, on April 24, 1954.

(vi) *Theobablia inconspicua*.—This species is a normal component of the mosquito complex of southern areas of this altitude. Our observations contributed nothing to knowledge of the biology of this species.

(vii) *Taeniorhynchus linealis*.—Adults of this species attracted to man were taken on ridges during February and April.

(viii) *Aedes alternans*.—Three specimens, one containing partly digested blood in its gut, were attracted to man during the dusk activity of April 6, 1954.

(ix) *Aedes* sp.—During subsequent investigations in March 1955 soon after a prolonged period of excessive rains, two females of the subgenus *Chironomomyia* were collected. They were attracted to human bait at site 1 during the dusk period.

(x) *Aedes albocinctus*.—The most striking larval characteristic of this species has been the infrequency of its occurrence in the relatively permanent rock-pool habitat coupled with its strong association with temporary ground pools. This in itself must lead to an erratic abundance which has also been reflected in adult catches.

Of the total catch of *A. albocinctus*, 23 per cent. has been collected from ridges compared with 5 per cent. for *A. pygmaea*. In part this difference may be due to the wider dispersal of the temporary breeding grounds of *A. albocinctus* which are not concentrated in places associated with adequate resting habitats. Even so, relatively more ranging does seem to be undertaken by *A. albocinctus*.

A. albocinctus is a sylvan species occurring independently of man and domesticated animals but attacking these as opportunity offers within or close to its natural habitat. Marsupials are an important natural blood source and it is also obvious that it attacks rabbits fairly freely. Feeding is well established for this species and it must undoubtedly assist in the spread of a disease such as myxomatosis.

Whether or not it has any special significance, during its peaks of abundance, in causing more than a low rate of transmission is not clear from the evidence collected.

(xi) *Aedes queenslandis*.—Although very closely related to *A. alboannulatus*, this species is rather more distinct biologically than morphologically. Its characteristic larval habitat is in rock-pools with a reasonable degree of permanency. Such rock-pools are usually polluted to a varying degree with leaf debris but this is not an essential characteristic. Breeding in ground pools does occur but to a considerably lesser degree; open tanks and wells are also utilized.

In the Mt. Flora area this species maintains itself throughout the year. Its abundance may fluctuate but there is always a significant larval and adult population. In fact, it is the dominant species of the area.

Adult activity occurs throughout the day in suitable places and in common with most of the other species apparently ceases shortly after dark. Its adult distribution covered most parts of the area even though it appeared less prone to ranging than *A. alboannulatus* (see above).

Its feeding habits are similar to those of *A. alboannulatus* but because of its higher and more constant population level, its significance in the carrying over of myxomatosis throughout all seasons of the year is far greater. The fact that it can find suitable habitats for breeding, feeding, and resting in rocky creeks with a reasonable amount of low vegetation and tree canopy may be of considerable importance when such an environment is either utilized by or is immediately adjacent to a rabbit population.

(xii) *Other Members of the Aedes alboannulatus Complex*.—One other member of this complex, as yet unnamed, but distinguished by the possession of a distinct sub-basal white band on the hind tibia, was collected in low numbers during March and April 1956.

(xiii) *Aedes notoscriptus*.—In total collections, this species parallels *A. alboannulatus* in abundance. Nevertheless, it was seen far less widely distributed as larvae, these being confined to the smallest of rock-pools very heavily polluted with leaf debris. This is another species which was fairly uniformly distributed throughout the year with more obvious larval and adult populations during the warmer months.

Significant adult activity was recorded from all habitats; it attacked freely during the day but its peak activity was undoubtedly during the early evening. Although it could be recorded as the first species attacking in the evening activity period, it was sometimes more active towards the end of the period and in certain places it was still being caught after general evening activity had ceased. Although substantial evidence of its ranging activity is presented in Table 14, it is not considered that any real appreciation of the behaviour of this species has been gained.

In addition to man, both marsupial and rabbit are attacked by this species but our information is too limited to suggest whether or not it may be of anything more than accidental importance in myxomatosis transmission.

On a later occasion, when we were attempting to feed mosquitoes on rabbits it was obvious that *A. notoscriptus* took every opportunity to feed at all times of the

day, either on the rabbits or the men handling them. From this it was concluded that it is an avid and not too discriminating feeder.* On the other hand, it is conceivable that use might be made of this species in certain habitats where rabbits occur but are not amenable to ordinary means of control. This suggestion is made because *A. notoscriptus* would be an easy species to stimulate to higher levels of population in forested gullies by the provision of artificial breeding habitats.

(xiv) *Aedes mallochi*.—A single specimen of the tree-hole breeding species *A. mallochi* was collected from human bait on March 4, 1956.

(xv) *Aedes biocellatus*, *A. monocellatus*, *A. subauridorsum*, and *A. quasirubithorax*.—No significance can be attached to the meagre recordings of these species other than that they represent new locality records.

(xvi) *Aedes vigilax*.—Although only 10 individuals of this species were taken they are of interest since the species is not known to breed at Mt. Flora, nor is it considered likely to do so. The nearest coastal and typical breeding grounds are from 20 to 22 miles to the east and these few females probably migrated that distance. The fact that they were only taken in February and March of the two successive years is also suggestive as this period coincides with the peak coastal activity of *A. vigilax* in the Sydney area. Four of the specimens were examined closely and gave a wing fringe ratio of 0 : 3 : 1 : 0 which is not inconsistent with the possibility of their having travelled a considerable distance. Individual records such as this are inconclusive but *A. vigilax* has been recorded from time to time at distances of from 20 to 40 miles from the eastern coastline and such records present the only really credible circumstantial evidence that we have had in Australia of mosquito movements of this magnitude.

The specimens collected came mostly from man during the evening activity period on the ridges or in Rocky Creek. What may be of significance, however, is that the remaining few came from rabbit-baited drop traps, or, on one occasion, vegetation close beside a trapped rabbit. The fact that rabbit feeding has been proved in our precipitin tests is at least suggestive and indicative of the need for further study of this species in strictly coastal environments.

(xvii) *Aedes vittiger*.—A single female of this species was collected biting man during an evening activity period. This species is widely distributed in eastern Australia and although Mt. Flora would not be considered one of its typical habitats, the same would apply to many of the places in which the species has been found in limited numbers.

(xviii) *Aedes rubrithorax*.—Two specimens taken during April 1954 merely provide a new locality record for this species. In a later very wet season (March 1956) with extensive opportunities for temporary water breeding, *A. rubrithorax* occurred in quite large numbers. They fed avidly on man and positive precipitin tests were also recorded for rabbit and possum feeding.

(xix) *Aedes burpengaryensis*, *A. flavifrons*, *A. macleayanus*, *A. nivalis*, *A. sagax*, *A. theobaldi*, and *A. bancroftianus*.—These species were all recorded attacking man in

* Prevailing conditions of humidity were relatively high on this occasion, and it has been the experience of one of us (D.J.L.) that *A. notoscriptus* is a species which is stimulated to unusually vicious attacks during the period of calm prior to the onset of storms.

quite low numbers during visits February 27–March 9, 1956, and April 24–29, 1956. Their appearance coincided with unusually extensive temporary surface waters caused by an extremely wet season. Larvae of these species were not taken.

(XXX) *Culex annulirostris*.—This species has a definite seasonal occurrence at Mt. Flora having been taken only during February, March, and April. Breeding has not been observed often but has occurred in grassy boggy habitats.

Adult catches have never been heavy, but they have come from all types of habitats. As elsewhere, it will attack in suitably sheltered situations during the daytime, but its main activity is in the early evening. It obviously ranges, and in evening catches it tended to be late biting and at times difficult to catch, more being seen after dark than would settle sufficiently to permit capture. On one occasion, this species was actively biting up to 2200 hr. All adults taken resting were females, under conditions indicating dispersal from breeding grounds.

The use of rabbit-baited drop traps during early February 1955 indicated that some rabbit feeding by *C. annulirostris* took place in the area. At the same time tubed specimens were also induced to feed on caged rabbits.

Since this species is known to be an important vector of myxomatosis elsewhere, and since its seasonal presence coincided with the time of our virus recovery from mosquitoes, the possibility that *C. annulirostris* played some part in this cannot be ignored, despite the lack of evidence.

(XXI) *Culex pipiens australiensis*.—This is the only species of *Culex* of any significance in the area.

It is certainly discontinuous in breeding and probably seasonal in occurrence. Its larvae were usually found in the leaf-printed margins of dams and creek pools with emergent grasses.

All adults collected were from resting habitats and this is one species frequently represented by gravid females in such sites. Ten females were collected from relatively inactive rabbit warrens, and this, together with the confirmation of its rabbit-feeding habit in the area, necessitate its consideration as a species contributing to myxomatosis transmission at Mt. Flora.

(XXII) *Culex fatigans*.—We did not concern ourselves with this typically domestic species as its biting activity away from artificial shelters is known to be quite limited. The species is probably well established in at least one of the homesteads. Elsewhere breeding was detected in heavily polluted water lying in a sheepyard. Subsequently (January 1956) one specimen was taken at site 2 amongst marginal timber.

(XXIII) *Culex pseudomelanoconia*, *C. fergusoni*, *C. postspiraculosus*, and *C. cylindricus*.—With these, there is no other significance than that they all occur in the Mt. Flora area.

X. OBSERVATIONS ON SANDFLIES (CERATOPOGONIDAE)

The two most obvious species in field collections were *Culisicoides marginimaculatus* over many months of the year and *Leptocneme stylus* in November only. A few other

species of *Culicoides* were occasionally taken attracted to man or in light-trap collections, but there is no reason for suspecting that they are of any significance. Another blood-sucking genus, *Lasiohelea*, also occurred.

(a) *Leptoconops stygius*

Nothing has so far been recorded of the habits of this inconspicuous but irritating biting fly. It occurs annually during the first two to three weeks of November in many of the sandstone gullies around Sydney and in parts of the Blue Mountains; it attacks man quite viciously around the head, particularly along the hair line. Poultry also are attacked.

The occurrence of this species at Mt. Flora has also been in November, but although attracted to man, it was not really a pest. Horses were most seriously attacked: up to 40 or more *Leptoconops* at a time were found biting inside the ear, causing a pronounced lumpy thickening of the ear itself. Rabbits, cows, and dogs were also attacked and the species was detected hovering around poultry.

Attack on rabbits was observed in drop-trap experiments and proven by precipitin tests on specimens caught both in this way and also attracted to man as bait. This last observation is indicative of a potentiality for double or multiple feeding and this being the case the species cannot be ignored as a possible myxomatosis vector during its annual period of abundance.

(b) *Culicoides magnimaculatus*

This species has been taken in variable numbers throughout the months November to June, and is probably of sporadic occurrence throughout the year: it is particularly abundant after prolonged periods of rain. At times its attack rate is high, at least on those individuals it chooses to bite: otherwise it is observed flying around the collector, particularly his boots. When abundant it may be collected in numbers with a sweep net.

A blood source predominantly attacked by this species was not revealed: the only positive precipitin test, other than for man, was a single possum reaction.

It does seem likely that, if this species attacked rabbits, some vestige of evidence would have been found. For the time being the possibility of it having played any part in myxomatosis transmission must be dismissed, even though a few individuals were taken attracted to rabbits in bait traps. These had not fed on rabbits and the attraction exhibited was no different from that occasioned by the observer's boots.

(c) *Other Culicoides spp.*

Seven additional known species of *Culicoides* and two undescribed species were also taken. Although several of these did attack man (see Table 10) most recoveries were from light-traps.

(d) *Lasiohelea townsvillensis*

Limited series of this species were collected at Mt. Flora attracted to both man and rabbits, and in light-traps. In other areas this species is known to be rather cryptic.

and the possibility remains that higher densities than we were able to detect may have occurred. We do not think that this species was of any importance in the transmission of myxomatosis; nevertheless, it is undoubtedly one which should receive further attention in an area suitable for such a study.

XI. OBSERVATIONS ON BLACK FLIES (SIMULIIDAE)

Four species from the two genera *Austrosimulium* and *Simulium* were collected. *S. ornatipes*, *S. melatum*, and *A. furiosum* were taken as larvae and pupae, and *A. furiosum*, *A. bancrofti*, and *S. ornatipes* as adults.

Twenty-five adult females of *A. furiosum* were attracted to man during spring and autumn months, and a single male was caught in a suction light-trap. They were never conspicuous and were observed only after a collector had remained static for some minutes. The species was not observed to attack any other animal. Although a few specimens commenced feeding on exposed legs they more usually hovered about, or rested fitfully on wet leather boots. Activity was observed at times ranging from 0930 hr till late dusk along the timbered ridges (sites 7 and 11) and in Rocky Creek (site 8). Warm sunny days seemed to be preferred but activity did occur during dull and overcast weather. Dusk activity was also observed, and it was on one of these occasions (March 25, 1954) that the species made its most determined and direct efforts to obtain human blood. This particular dusk period featured a most pronounced convection of warm air. Larvae were collected once in association with *S. melatum* from a sluggish stream running over large water-worn stones in the bed of Upper Stockyard Creek (between sites 3 and 5).

A. bancrofti, the next most frequent adult species (8 specimens) was collected from the belly of a horse grazing on open pasture and once from man in thick scrub with heavy undergrowth. This species was active during spring and autumn on warm sunny days. Immature stages were not collected.

Although the early stages of *S. ornatipes* were more frequently collected than those of other species, no adult females were taken. A single male was caught in a suction light-trap. Larvae and pupae were almost always present in Stockyard Creek (site 3) on grass blades, water-worn rocks, and dead leaves caught amongst the rocks. They occurred frequently in association with *S. melatum*. The apparent absence of adults of *S. ornatipes* when early stages were most abundant has been reported previously by Mackerras and Mackerras (1948).

No adults of *S. melatum* were taken although its early stages were present in Stockyard Creek during the late summer and autumn months and were collected from the Nattai R. in April (site 10).

The permanent stream of Stockyard Creek provides the most favourable breeding place for species of this family in the study area. Larvae were seen only once in the other creek system, Flora's Gully, following the abnormal flood rains of February 1955, which caused the creek to run freely for a longer period than usual.

Mykutowycz (1957) implicated *S. melatum* as a vector in myxomatosis epizootics on the Murray River flats during 1951. There is no evidence that any of the species occurring at Mt. Flora were involved in any way, nor is the possibility considered very likely.

Observations during March 1956 revealed black fly activity far greater than previously recorded in the area. Explanation of this increase undoubtedly lies in the availability of breeding waters created by prolonged abnormal rains. These subsequent observations were mainly restricted to a timbered transect running from about 200 yd south of site 1 down the slope to site 11, and during the late afternoon and dusk period.

A. furiosum and *A. bancrofti*, as well as attacking man, fed on rabbits exposed below drop traps. In addition to these two species more frequently collected, a single specimen of *S. melatum*, one *Simulium* sp. (*clathrinum* group), and four and 16 of each of two species of *Cnephia* were taken. The two *Simulium* spp. were attracted to human bait while the latter two species fed on both man and rabbit.

XII. OBSERVATIONS ON MARCH FLIES (TABANIDAE)

From the Mt. Flora area, 10 species of Tabanidae have been collected, with an additional two undescribed species and two varietal forms which may eventually rank specific status. (The undescribed and dubious material will be dealt with later in a revision of the family now being undertaken by Dr. I. M. Mackerras.) The recorded species have been listed in Section VIII.

Tabanidae were only collected during the months November to April of the three summer periods of our observations, and almost always when attacking man. Activity was most pronounced on humid sunny days on the lower timbered ridges and cleared grazing areas. An abundance of adults was not invariably associated with such weather, nor did apparently bad weather prevent activity though it did seem to reduce it. Specimens were attracted to man and horse from 1000 to as late as 1700 hr. Cattle, when observed, were seriously attacked but it was not possible to collect from these animals although an engorged specimen taken at a window did yield an ox-positive precipitin test.

Cattle provided the most important blood source for Tabanidae at Mt. Flora and the considerable agitation of cattle under heavy attack undoubtedly results in a much reduced food intake. Further, in the opinion of the local residents, milk yields are seriously reduced during the periods of maximum March fly activity.

Although a single specimen of *Cydistomyia* sp. was experimentally tube-fed on a caged rabbit, there is no real evidence that rabbits are attacked by any species of Tabanidae.

XIII. OBSERVATIONS ON LEPTIDAE (RHAGIONIDAE)

Two species of the blood-sucking genus *Spaniopsis* were taken, namely *S. longicornis* and *S. vexans*. They were characteristically present during the autumn months only, the former being recorded in the months of February, April, and June, but especially at the end of April, and the latter in March and April. *S. longicornis* appeared to predominate in this area, most of the collections made being of this species.

Both species were relatively inconspicuous, and were usually not observed until a collector remained static for some minutes. Their attack was seldom vicious but they were very prone to investigate the face and in particular the nose, although probing seldom took place. Engorged specimens were not recovered, nor were these flies observed on animals other than man.

XIV. CONCLUSIONS

(1) Mt. Flora is a rabbit-populated grazing area surrounded by virtually rabbit-free virgin scrub and forest. It is typical of many hill-stream environments near the watersheds of streams discharging to the coast, although with a considerably larger area of clearing than most. The biological relationships of the biting-fly complex and rabbits as observed at Mt. Flora should be comparable to that obtaining in other similar areas in which considerable physical difficulties confront the problem of rabbit eradication.

(2) Myxomatosis was introduced into the Mt. Flora area late in 1952, at a time of high rabbit density. At no stage during 1953 could we detect a serious epizootic but from shortly after the introduction of the disease there was a continuous occurrence of myxomatosis at all seasons of the year for at least 18 months. Following this, no evidence of disease was detected until the commencement of a severe epizootic in February 1955.

(3) The effect of the disease during the first outbreak period was difficult to estimate, but during the first 12 months it is considered to have been responsible for a significant decrease in the total rabbit population. This decrease was reinforced by trapping, which was employed rather more exhaustively than in most areas even though only one trapper was engaged. The relative importance of disease and trapping cannot be accurately assessed but our considered opinion is that each contributed approximately equally to the reduction of the rabbit population to negligible proportions. Recovery of the population took place very slowly, but by the 1954-55 summer rabbits had again become competitors for pasturage. The effect of the succeeding epizootic was uncomplicated by any other rabbit control activities. It was obvious, effective, and rapid, resulting in a reduction of population of a very high order with very little recovery in the following 12 months.

(4) During the first epizootic period virus recovery from wild-caught Culicidae, Ceratopogonidae, and Tabanidae was attempted. This resulted in two recoveries of virus from mixed collections of *Aedes queenslandis* and *A. alboannulatus* this being the first occasion on which either of these species has been shown to be a vector of myxomatosis.

(5) In the Mt. Flora area over 60 species of biting flies occur, belonging to the Culicidae, Ceratopogonidae, Simuliidae, Tabanidae, and Leptidae. Of these, nine species of Culicidae (*Anopheles annulipes*, *Tripteroides* sp., *Aedes alboannulatus*, *A. queenslandis*, *A. notoscriptus*, *A. rubrithorax*, *A. vigilax*, *Culex annulirostris*, and *C. pipiens australicus*) and two of Ceratopogonidae (*Leptoconops stygius* and *Lasiohelea townsvillensis*) have been shown to attack rabbits.

(6) The mosquito population is dominated by the species *A. queenslandis* and *A. alboannulatus*. The abundance of the former is relatively constant throughout the year, its breeding habitats being permanent in character. The latter fluctuates considerably in abundance being largely dependent on temporary breeding grounds. This could lead to the facile suggestion that *A. alboannulatus* is of more epizootic significance and *A. queenslandis* important in disease carry-over, but such a simple suggestion has received little support from our various observations.

(7) There is no doubt that myxomatosis is carried over, in even a greatly reduced rabbit population, for periods well in excess of 12 months. Adequate wintertime trappings of affected rabbits have proved a continuity of transmission throughout the colder periods of the year. In the Mt. Flora area the only mosquitoes likely to occasion such transmission are *A. notoscriptus*, *A. alboannulatus*, and *A. queenslandis*. So far, circumstantial evidence is strongly in favour of *A. queenslandis* as the important carry-over vector.

(8) One of the most important observations made in the Mt. Flora area is that even at an altitude of approximately 2000 ft there is no winter cessation of mosquito activity. There is a general reduction of activity but within the complete habitats the difference between winter and summer activity is not marked.

Nevertheless, some species are seasonal and this applies particularly to the species of *Culex*, others are erratic such as *A. alboannulatus*, most would be considered rare, but a few such as *Anopheles annulipes* and *Aedes notoscriptus* also fluctuate but within limits narrower than those of *A. alboannulatus*.

(9) From our observations of activity and blood sources it is inferred that myxomatosis is probably transmitted by all the mosquito species found feeding on rabbits at Mt. Flora. Nevertheless, the dominant vectors of the western rivers, *Anopheles annulipes* and *Culex annulirostris*, are not sufficiently abundant to be important in epizootic disease incidence. Nor have any of the species recorded attacking rabbits shown themselves to be highly selective of rabbits as a blood source and hence are not likely to be important for this reason alone.

(10) There is no evidence to suggest that biting flies other than Culicidae played any part in myxomatosis transmission in the Mt. Flora area.

(11) Our observations showed that adult mosquitoes could be found over almost the entire study area but significant differences in population density and activity were associated with different ecological zones. Rocky creeks with some ground cover and a low canopy provided complete habitats for mosquito activity but this was not the case with any of the more open creeks. Areas of reasonably dense ground cover 3-4 ft high associated with a fairly open canopy provided diurnal resting zones. All other areas, either treeless or open forest with no ground cover, were only productive of mosquitoes during peak activity periods.

(12) Adult mosquito activity in complete habitats could be recorded at most times of the day. Sometimes it was in the form of a definite attack on the collector, at other times the collector seemed to be intercepting a moving population. The most intense diurnal attacks were associated with high atmospheric humidities and low illumination.

Limited diurnal activity was frequently observed in resting zones. Provided collectors remained stationary for about ten minutes attack would usually be recorded but the self-limiting character of this attack made it apparent that the attraction of the collector was being exercised over a limited radius.

(13) The most characteristic period of generalized activity took place in the early evening and most of the species commonly collected participated. This evening

activity period occurred about the time of sunset and was seldom of more than 2 hr duration. Within this period, a shorter one, usually of less than 30 min, was characterized by an intensification of biting activity. Under favourable conditions this evening attack could be experienced in most types of habitats, indicating a general ranging movement of the mosquito population. The termination of this activity period was uniform, even in complete habitats.

Some day-to-day variations in onset, duration, and intensity certainly occurred. The factors of humidity, temperature, illumination, and air turbulence were all involved but the most dramatic intensification appeared to be associated with the incidence of convection currents within 4 ft of ground level.

(14) Because we were unable to detect any correlation between species abundance, either on an individual or collective basis, and epizootic incidence of myxomatosis, and because such incidence has been confined to the autumn period in coastal and tableland areas of southern New South Wales and eastern Victoria, we have been constrained to believe that the explanation of epizootic incidence lies in a seasonal behaviour pattern of the vectors. Or, more strictly, that some form of behaviour, possibly meteorologically determined, which occasions wider contact between mosquitoes and rabbits, occurs with greater regularity during the autumn period.

(15) In considering the individual species present at Mt. Flora, the following points were worthy of note:

- (i) *Aedes queenslandis*: The fact that *A. queenslandis* finds a complete habitat for all its activities in sheltered, vegetated rocky creeks, that it occurs throughout the year, and that it is by no means averse to feeding on rabbits may be of importance in the selection of sites for inoculation of myxomatosis virus in the future. A seeding in such an area should be independent of seasonal vagaries and maintenance of the disease should be possible between epidemic periods. In any case observations of mosquito activity at Mt. Flora would indicate the desirability of careful selection of a site for seeding of the virus in any given area, rather than the usual choice of the most readily available rabbits.
- (ii) *Aedes notoscriptus*: This species commonly attacks rabbits and is almost as permanent an inhabitant of complete habitats as *A. queenslandis*, though subject to greater fluctuations in population density. It could readily make an important contribution to myxomatosis transmission and is the one species amenable to artificial increasing of population density.
- (iii) *Aedes vigilax*: Although this species was rarely taken, evidence of its attack on rabbits was obtained. This, coupled with the fact that it can fly considerable distances, may have some significance in disease movement in coastal areas.

(16) The information gained during periodic visits to the area has been cumulative. What was particularly interesting, however, was the gradual increase of records of blood-sucking species of flies to a present total of over 60 species, and it is unlikely that the possibilities have been exhausted.

XV. ACKNOWLEDGMENTS

In the scientific part of these investigations we are indebted to a number of colleagues for cooperation in their special fields. Virus and immunity testing have been carried out by Professor F. Fenner and Dr. I. D. Marshall, Department of Microbiology, John Curtin School of Medical Research, Australian National University. Precipitin tests have been done by Mr. K. J. Clinton, School of Public Health and Tropical Medicine, University of Sydney. Identifications of Simuliidae and Tabanidae have been provided by Dr. I. M. Mackerras, Queensland Institute of Medical Research, and botanical identifications by Mrs. Alma T. Lee.

Early observations of rabbits were undertaken by Dr. R. Mykytowycz, and marsupials identified by Mr. B. J. Marlow, both of the Wildlife Survey Section, C.S.I.R.O. Assistance in the field has been contributed by Messrs. F. N. Ratcliffe, C. Brooker, L. MacLean, and M. N. Dennis, all of the Wildlife Survey Section, G. Sackelariou, Division of Entomology, C.S.I.R.O., and K. G. Brown, J. J. Lawrence, J. G. Somerville, and J. Citowitsch, all of the School of Public Health and Tropical Medicine, University of Sydney.

Figures 1-3 were prepared by Mr. L. A. Marshall, Division of Entomology, C.S.I.R.O.

Beyond these we must record our deep indebtedness to Messrs. Sidney, Dudley, and Henry Blatch, the three farmers located on the study area. All three gave us ready assistance and extended our background observations on the rabbit population over the periods we were not present in the area. Our more detailed observations were made on the property of Mr. Henry Blatch who willingly provided us with every facility at his disposal.

We are also beholden to Mr. I. L. Jurd, a resident of Colo Vale, who kindly provided us with detailed rainfall registrations.

XVI. REFERENCES

- DEPARTMENT OF LANDS (1946).—Homoclimatic map of New South Wales Forestry Commission—Sydney region. (Dept. of Lands: Sydney.)
- EDWARDS, F. W. (1924).—A synopsis of the adult mosquitoes of the Australasian region. *Bull. Ent. Res.* **14**: 351-401.
- FENNER, F., MARSHALL, I. D., and WOODROOFE, GWENDOLYN M. (1953).—Studies in the epidemiology of infectious myxomatosis of rabbits. I. Recovery of Australian wild rabbits (*Oryctolagus cuniculus*) from myxomatosis under field conditions. *J. Hyg.* **51**: 225-44.
- FENNER, F., and MARSHALL, I. D. (1957).—A comparison of the virulence for European rabbits (*O. cuniculus*) of strains of myxoma virus recovered in the field in Australia, Europe and America. *J. Hyg.* **55**: 149-91.
- MACKERRAS, I. M., and MACKERRAS, M. J. (1948).—Revisional notes on Australasian Simuliidae (Diptera). *Proc. Linn. Soc. N.S.W.* **73**: 372-405.
- MYERS, K., MARSHALL, I. D., and FENNER, F. (1954).—Studies in the epidemiology of infectious myxomatosis of rabbits. III. Observations on two succeeding epizootics in Australian wild rabbits on the riverine plain of south-eastern Australia 1951-1953. *J. Hyg.* **52**: 337-60.

- MYERS, K. (1956).—Methods of sampling winged insects feeding on the rabbit, *Oryctolagus cuniculus* (L.). *C.S.I.R.O. Wildl. Res.* **1**: 45–58.
- MYKYTOWYCZ, R. (1957).—The transmission of myxomatosis by *Simulium melatum* Wharton (Diptera: Simuliidae). *C.S.I.R.O. Wildl. Res.* **2**: 1–4.

EXPLANATION OF PLATES 1 AND 2

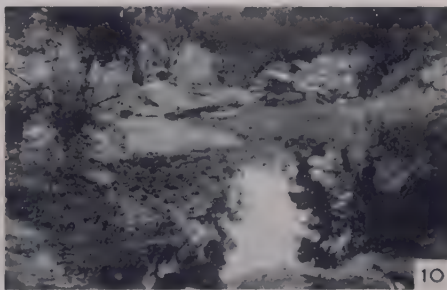
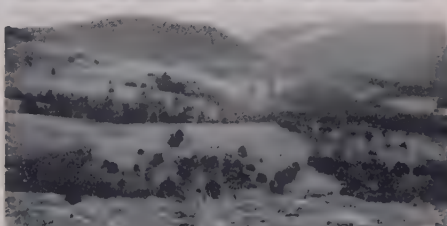
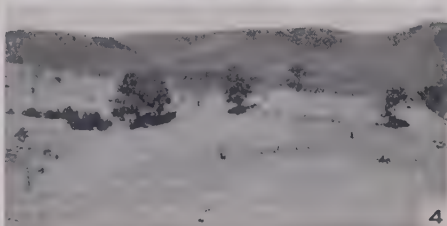
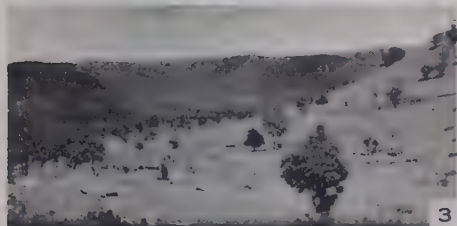
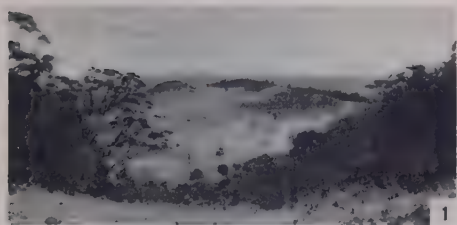
PLATE 1

- Fig. 1.—View from the point of entry to the study area looking towards Mt. Blatch over the elevated, exposed grazing area on which are situated the three homesteads. The gap in the trees in the foreground (site 20, Fig. 3) leads down to the area shown in the photograph immediately below.
- Fig. 2.—The grazing land of intermediate elevation and more gentle slope is shown in this photograph taken from the exposed saddle looking at the rugged country across the Nattai R. The cleared country in this photograph extends from site 17 to site 2 in Figure 3.
- Fig. 3.—The summit of Mt. Flora appears on the right. The foreground is one of the more gently sloping saddles of the upper cleared area and eventually falls over steep cleared slopes to Stockyard Creek.
- Fig. 4.—This view from near site 17 of Figure 3 shows in more detail the hillock just appearing in the right-hand bottom corner of the photograph immediately above.
- Fig. 5.—The crest of Mt. Flora (site 19, Fig. 3) appears at the left. The distant conical peak is Mt. Jellore. One of the limited cultivated areas is visible in the distant foreground. The polluted water-hole lies just beyond the far corner of the cultivation adjacent to the base of Mt. Flora.
- Fig. 6.—The central peak is Mt. Blatch. In the foreground are the excavated dams at site 18 of Figure 3.
- Fig. 7.—This view is taken from near site 13 (Fig. 3) looking towards sites 15 and 16. Site 13 lies within the dense thicket in the middle foreground.
- Fig. 8.—Taken from just above site 16 of Figure 3, this panorama looking towards Stockyard Creek shows the typical disposition of timbered areas breaking the continuity of the cleared grazing areas.
- Fig. 9.—This is site 13 of Figure 3. Mt. Flora is in the distance and the gully is one of the upper branches of Flora's Gully. It is at this crossing in the foreground that seepages maintain permanent pools.
- Fig. 10.—A similar site to Plate 1, Figure 9, on another upper branch of Rocky Creek (site 12 of Figure 3). Here again, seepages maintain permanent pools of moderate size with emergent vegetation in muddy margins.

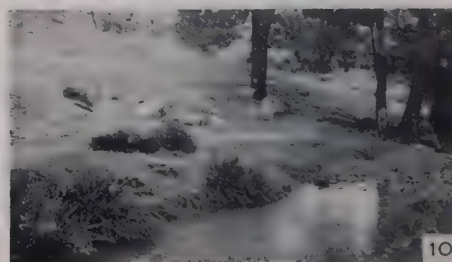
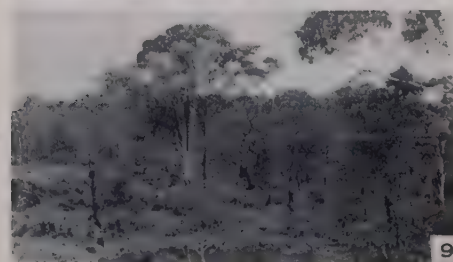
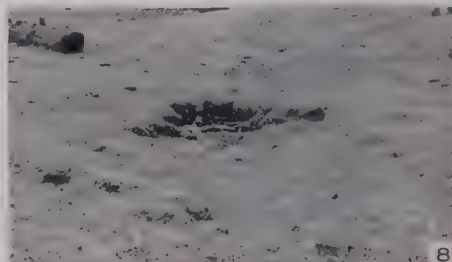
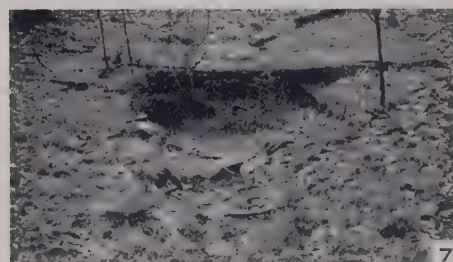
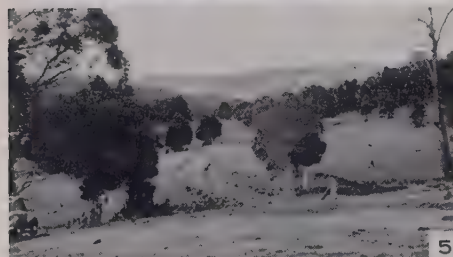
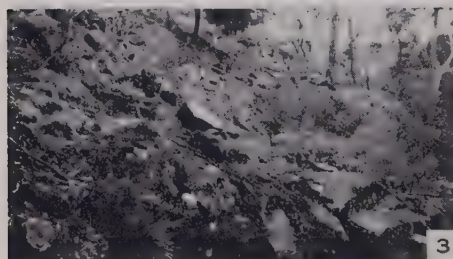
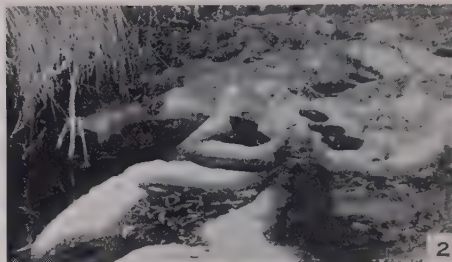
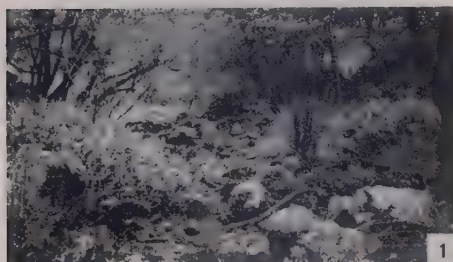
PLATE 2

- Fig. 1.—Rocky Creek. This is one of the dry sections below that shown in Plate 1, Figure 10. The dominant vegetation is herringbone fern at ground level and the canopy is provided by grey myrtle. This area was extensively utilized as an adult catching site.
- Fig. 2.—A section of Rocky Creek about 100 yd below Plate 2, Figure 1. This zone provided many small and large rock-pools which were continuously breeding mosquitoes.

MYXOMATOSIS TRANSMISSION IN A MOUNTAIN ENVIRONMENT



MYXOMATOSIS TRANSMISSION IN A MOUNTAIN ENVIRONMENT



- Fig. 3.—This view shows the nature of the terrain forming the gully of Rocky Creek. Rocky banks of this nature led to both sites shown in Plate 2, Figures 1 and 2.
- Fig. 4.—A typical small thicket of paper-barks. This one was in the general area of site 1 of Figure 3.
- Fig. 5.—A view from site 1 (Fig. 3) looking back to site 17 on the skyline.
- Fig. 6.—This is in the same general direction as Plate 2, Figure 5, but shows the permanent earth dam in the area of site 1 of Figure 3.
- Fig. 7.—A temporary pool typical of the general area around site 2 of Figure 3, formed in one of the drainage lines of the lower ridges.
- Fig. 8.—A temporary pool in a drainage line across the grazing area in the vicinity of site 1 of Figure 3.
- Fig. 9.—This is one of the ridges (site 2, Fig. 3) on which evening collections were frequently made.
- Fig. 10.—Stockyard Creek at site 3 of Figure 3. This is typical of a long stretch of this creek and should be contrasted with the typical views of Rocky Creek shown in Plate 2, Figures 1 and 2.

BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS (MYGALOMORPHAE : CTENIZIDAE)*

By BARBARA Y. MAIN†

[Manuscript received May 6, 1957]

CONTENTS		Page
Summary		403
I. Introduction		403
II. Methods		404
(a) Collecting methods		404
(b) Laboratory methods		404
(c) Taxonomic methods		406
III. Systematic synopsis		407
(a) Diagnosis of the tribe Aganippini		407
(b) Taxonomic limits of the tribe		409
(c) Synopsis of genera and species		415
(d) Identification key		441
IV. Natural history		442
(a) Life history		442
(b) Habitat preferences and ecological distribution		444
(c) Geographical distribution of the species		446
(d) Construction and maintenance of burrows		447
(e) Burrow associates		449
(f) Habitat selection		449
(g) Defence behaviour		450
(h) Predators and parasites		453
(i) Feeding biology		454
V. Morphology and behaviour		457
(a) Morphological trends (adaptive characters)		457
(b) Correlation of morphological trends		460
(c) Trends in structure of male external genitalia		461
(d) Correlation of morphology and behaviour		461
VI. Evolution		461
(a) First phase of the radiation		464
(b) Second phase of the radiation		464
(c) Third phase of the radiation		469
VII. Acknowledgments		471
VIII. References		472

*Part of a thesis submitted to the University of Western Australia, in partial fulfilment for the degree of Doctor of Philosophy.

†Zoology Department, University of Western Australia, Nedlands, W.A.

Summary

A taxonomic revision of the tribe Aganippini (Ctenizidae) is made. The genus *Blakistonia* Hogg is excluded from the tribe, *Gaius* Rainbow is synonymized with *Anidiops* Pocock, and *Eucyrtops* Pocock is re-instated. The group now consists of the four genera *Aganippe* Cambridge, *Idiosoma* Ausserer, *Anidiops*, and *Eucyrtops*. The former 23 species of the tribe are reduced to nine, and three new species are described, making a total of 12 valid species. Allotypes of five species, previously known only from one sex, are designated and described.

Many characters customarily used in mygalomorph taxonomy are criticized and shown to be inadequate.

Observations on the life histories and natural history of the species are recorded. The adaptive function of different burrow and door structures is discussed. Distribution of species in relation to particular habitat types in the general environment is mentioned. Parallel adaptation of a specialized foraging behaviour ("twig-lining", whereby spiders attach twigs to the rim of the burrow in such a way that they are utilized as "feeling lines" when foraging) is recorded for seven species in three genera. Twig-lining appears to be an adaptation to relatively dry habitats where the food supply is less abundant. By this method of foraging, animals increase their area of search for food.

A relationship between morphology and behaviour is noted. Certain morphological features, in particular the eyes, are shown to be correlated with burrow structure, including door type, and foraging behaviour.

The evolutionary radiation of the tribe is shown to be the result of ecological expansion. Postulated phylogeny of the tribe is outlined.

Derivation of the genus *Idiosoma* from *Aganippe* is postulated. It is suggested that this has been due to "block" inheritance of several characters (which together have adaptive superiority), and which are assorting independently in other species. These characters, when inherited together, mark the irreversible culmination of the adaptive trend of twig-lining, the initial stages of which are exhibited by the adaptively plastic species of *Aganippe* and *Anidiops*.

I. INTRODUCTION

Earlier studies on Australian Mygalomorphae were primarily systematic and were generally based on material intermittently received by museums and for which there was little accompanying biological information. With the exception of Hickman in his many papers and Rainbow and Pulleine (1918) the authors of the systematic accounts usually failed to report on, or had no knowledge of, the field occurrence of the specimens. However, even where biology has been reported a comprehensive comparative biological study of any group has not been previously attempted.

The present study deals with the comparative biology of the Aganippini (Ctenizidae: Ctenizinae), the dominant group of trapdoor building Mygalomorphae in southern Australia west of the Flinders Range. The following account is based on comprehensive field collections made by the present author over a period of four years. Collections were planned so that as much knowledge as possible was gained on distribution, ecology, and behaviour of these spiders. As biological and field data accumulated it became apparent that a taxonomic revision of the group would need to be made before or along with analysis of the biological information.

This paper reviews the taxonomy, presents observations on the natural history, demonstrates the close relationship of morphology and behaviour, and interprets the evolution of the group as an autochthonous ecological radiation.

II. METHODS

(a) *Collecting Methods*

Mygalomorphae are commonly regarded as difficult to collect because of their cryptozoic habits and sometimes exaggerated fossorial tendencies. However, this difficulty was easily overcome. Burrows hidden by wind-blown soil or dense leaf litter were exposed by slicing the soil surface with a spade. Spiders were recovered by dissecting the burrow into a vertical pit dug alongside. From the vertical burrow section thus exposed dimensions were recorded, food debris collected, and the burrow characteristics noted.

The door and burrow entrance was always collected with the associated spider. Entrances were stuffed with cotton wool before being cut out of the soil and were then either wrapped in crêpe paper and placed in a chippet box or were bound with moistened plaster of paris bandage. Specimens so strengthened were easily transported and stored.

Rejectamenta containing identifiable remains of arthropods were usually found deposited as plugs along the sides and bottom of the burrow.

Notes were made systematically on all specimens and their burrows. The main environmental features recorded were soil type, litter type, general vegetation and particular plants with which the burrows may have been associated, and the topographical situation of the habitat. Specimens, doors, and food debris all had a comparable field note. For laboratory convenience these specimens later received an additional serial catalogue number.

Field collecting followed a rigorous plan to gain a broad outline of the geographical limits and ecological distribution of all species, excursions being planned on the basis of known physiographical and vegetational zones. In spite of alteration of much of the country by agricultural development, specimens were collected from intensively farmed and grazed areas by persistently searching in remnant habitats such as along roadsides and corners of paddocks, or wherever a few trees of the natural vegetation remained. Thus, in spite of the partial destruction of many of the spider habitats, it has still been possible to define the main distributional limits of the mygalomorph species, and to obtain an idea of the ecological preferences.

(b) *Laboratory Methods*

(i) *Biology*.—Living specimens collected in the field were sometimes returned for observation to the laboratory where they were maintained in large earthenware flower pots filled with soil and covered with sheets of glass, in a room controlled at 75 F. Methyl hydroxybenzoate was used to prevent fungus infections. Some specimens have been maintained for over three and a half years and are still flourishing. One of these specimens has been mated in the laboratory, and it has subsequently produced young which in turn have made burrows of their own.

(ii) *Measurements and Drawings*.—All diagnostic work on preserved material was done with the aid of a Zeiss Opton microscope. Drawings were made free-hand on squared paper while viewing the specimen with a micrometer containing a squared graticule. All figures of male palps are of the right palp viewed retrolaterally, so that figures can be directly compared.

(iii) *Material Examined*.—The present study is based almost entirely on the author's collection of more than 1400 specimens of which all but a few dozen were collected personally in the field. In addition, the available type material in the

TABLE I
CARAPACE LENGTH OF REPRODUCTIVELY ACTIVE FEMALES* SHOWING RANGE
OF SIZES WITHIN AND BETWEEN SPECIES

Species	Range of Carapace Lengths (mm)	No. of Specimens
<i>Eucyrtops latior</i>	5.00- 7.50	3
<i>E. cremona</i>	3.70- 3.90	2
<i>E. riparia</i>	4.80- 8.70	21
<i>Eucyrtops</i> , "spinular" form	7.70-13.00	3
<i>Arctops unaristipes</i>	6.50-10.50	4
<i>Ar. ciliatus</i>	18.00	1
<i>Aganippe submissus</i>	9.20	1
<i>Ag. swainsoni</i>	10.40	1
<i>Ag. occidentalis</i>	5.40-10.20	8
<i>Ag. caprimona</i>		
Type race	8.00-10.50	26
Rottneest race	5.50- 7.10	2
Twig-lining race	4.20-10.50	3
Proto- <i>Idiosoma</i> race	9.10	1
Type proto- <i>Idiosoma</i> race		
intermediates	10.00-10.50	3
<i>Ag. cupulifera</i>	7.00- 9.80	13
<i>Idiosoma sigillatum</i>	11.50-14.00	3
<i>I. nigrum</i>	8.50- 9.30	4

* I.e. specimens with either eggs or broods in the burrow.

Australian Museum and the South Australian Museum has been examined, together with a few specimens in the National Museum and one specimen in the Queensland Museum. Finally, the collection of the Western Australian Museum has been examined, two specimens of which are here designated allotypes of earlier described species.

(iv) *Deposition of Specimens*.—All types designated in this study, together with representatives of the other species discussed, have been deposited in the Western Australian Museum. Apart from these specimens the bulk of the collection on which this study is based are retained in the author's working collection at the Zoology Department, University of Western Australia.

(c) *Taxonomic Methods*

Some of the morphological characters customarily used in systematics were found inadequate to delimit natural groups in the Aganippini. This is partly due to certain peculiarities in the life history of mygalomorph spiders. The longevity of mygalomorphs is well known and Baerg has documented the life span of theraphosid individuals. For laboratory specimens he states that some females take 10 years to mature, and also that some females which had not produced eggs lived in the laboratory for at least 11 years after maturity (Baerg 1945, p. 106).

Since specimens (at least females) continue to grow and moult after maturity an analysis of characters likely to be modified with age, was made. The most significant of these will be discussed.

TABLE 2
RANGE OF CARAPACE LENGTHS OF MALE SPECIMENS

Species	Range of Carapace Lengths (mm)	No. of Specimens
<i>Eucyrtops latior</i>	4.40- 6.70	4
<i>E. eremaea</i>	3.10- 3.70	6
<i>E. riparia</i>	4.20- 5.50	9
<i>Eucyrtops</i> , "spinular" form	4.40	1
<i>Anidiops manstridgei</i>	7.90	1
<i>An. villosus</i>	12.00-14.50	12
<i>Aganippe subtristis</i>	5.80- 9.20	2
<i>Ag. raphiduca</i>		
Type race	5.80- 7.50	9
Rottnest race	4.30- 5.00	2
Proto- <i>Idiosoma</i> race	8.90	1
Twig-lining race	6.60- 8.40	3
Type/proto- <i>Idiosoma</i> race intermediates	6.60- 9.50	3
Aberrant form	5.20	1
<i>Ag. cupulifex</i>	4.60- 6.90	8
<i>Idiosoma sigillatum</i>	8.40-10.50	6
<i>I. nigrum</i>	6.90- 9.00	9

(i) *Size as a Diagnostic Character*.—Although females of a species probably have a characteristic maximum size and the mean adult size for females of a species can be obtained, the degree of overlap for the various species does not permit size to be *generally* used as a diagnostic character. Ranges in size of reproductively active females are presented in Table 1.

Individual male specimens of mygalomorph species mature at different sizes. The range in length of carapace of mature undamaged male aganippine specimens of each species examined by the author is presented in Table 2. Gross size, when not considered in conjunction with other characters, is *usually* of little diagnostic value for male specimens of Mygalomorphae.

(ii) *Countable Characters*.—The marked variability of the number of cheliceral teeth in valid biological species of mygalomorphs led the author to review this

feature and other countable characters as worth-while diagnostic characters. Accordingly, the teeth of each of the 3 rows along the groove of the right chelicera were counted on 73 specimens of *Eucyrtops latior* (Cambridge) (for revised position of this species see Section III) of various sizes taken at random. The number of teeth on the inner, outer, and intermediate rows were then plotted against the carapace length of the specimen. It was found that the number of teeth (particularly of the intermediate row) tended to increase with the size of the animal. These data are presented in Table 3.

A cursory examination of the cheliceral teeth of the other aganippine species revealed similar trends. Rastellum teeth and maxillary cuspules possibly exhibit the same tendency. Such characters are therefore not good diagnostic features.

In descriptive taxonomy much attention has been paid to the particular number of spines and their position on leg segments. The value of this (at least for Mygalomorphae) is questioned, since such descriptions are usually based on one or at the most a few specimens.

In the Aganippini, spines occur on leg segments as indicated in Tables 4 and 5 which are based on 72 specimens of *E. latior* and 46 specimens of *E. riparia*, sp. nov., these being specimens of various sizes and taken at random.

These results emphasize both infraspecific variability and interspecific overlap and therefore indicate the questionable value of giving lengthy spine formulae in species descriptions based on few specimens.

(iii) *Adaptive Variation of Certain Morphological Features.*—These include such features as relative measurements and distances apart of eyes, and leg lengths and their relative thicknesses. The present study indicates that these characters vary adaptively (see Section V). Parallel modification of eyes and legs occurs within the various species, consequently adaptive extremes of two species may by convergence be indistinguishable morphologically.

It is difficult to find consistent characters by which the species can be diagnosed. The approach of the present study has been essentially biological, and morphological differentiation of species and genera was secondarily investigated. Zoologists are now beginning to use behavioural characters in taxonomic studies. Delacour and Mayr (1945, p. 49), in their review of the family Anatidae, state: "Biological characters are of paramount importance to the classifier, for habits and behaviour are certainly deeply rooted and are often the product of a very ancient evolution." Again, Evans (1953), in his review of comparative ethological studies, illustrates with an example from spider wasps his contention that behavioural characters are of great value in systematics.

III. SYSTEMATIC SYNOPSIS

(a) *Diagnosis of the Tribe Aganippini*

The Aganippini are an endemic Australian tribe of the family Ctenizidae, subfamily Ctenizinae. Morphologically the group is distinguished principally by a combination of the following two features:

- (i) The eyes which are arranged in 3 clearly defined rows, consisting from anterior to posterior of 2, 2, and 4 eyes.

TABLE 3
NUMBER OF CHELICERAL TEETH PRESENT ON INNER, OUTER, AND INTERMEDIATE ROWS OF THE RIGHT CHELICERA OF 73 SPECIMENS
OF EURYPTOPS LATIOR
The animals are grouped according to carapace length which is taken as a measure of gross size and presumably age of the animal

No. of Teeth on:

Carapace Length mm.	Inner Row					Outer Row					Intermediate Row												
	5	6	7	8	4	5	6	7	8	9	10	2	3	4	5	6	7	8	9	10	11	12	13
2.0-2.9	5				3	1	1					4		1									
3.0-3.9	5	7	2		1	4	7	2					9	4	1								
4.0-4.9	1	12	2		1	4	6	2	1	1			4	7	3	1							
5.0-5.9		5	3	1		1	4	2						1	6		2						
6.0-6.9		11	4	1		3	4	5	2	1	1			1	6	3	4	2					
7.0-7.9		2	4	1		1	1	1	3	1					1	3	1	2					
8.0-8.9		2	1			3									1		2		1				
9.0-9.9			1						1	1	1												2
10.0-10.9		1									1						1						

- (ii) The shape of the labium, which is relatively short and broad and is broadly indented anteriorly (Fig. 1B); this is in contrast with the more elongate, almost straight-sided labium of other Australian Ctenizinae (Fig. 1A), such as *Blakistonina*.

(b) *Taxonomic Limits of the Tribe*

The five genera—*Idiosoma*, *Aganippe*, *Anidiops*, *Gaius*, and *Blakistonina*—have traditionally been accepted in the literature as a phylogenetic group, included under the name *Aganippeae*.

Ausserer (1871, p. 150) proposed the genus *Idiosoma* to contain Cambridge's species *Idiops sigillatum*, which had been described from a single dried male specimen. Ausserer considered the sclerotized, corrugated abdomen to be a feature denoting generic standing. Simon (1892, p. 91) removed the species to the genus *Acanthodon*, inferring that the nature of the abdomen was merely a sexual difference. However, Pocock (1897, p. 109) had a female specimen which obviously belonged to the same species as the male *sigillatum*. Along with other structural similarities this female specimen had a strongly corrugated abdomen and on this basis Pocock re-instated the genus *Idiosoma*.



Fig. 1.—Labia of Ctenizinae. A, *Blakistonina* Hogg; B, aganippine.

Meanwhile, Cambridge (1877, pp. 28–9) had erected another genus, *Aganippe*, to contain two species—*subtristis* and *latior*. Pocock (1897, p. 113) removed *latior* from *Aganippe* and proposed for it a new genus *Eucyrtops*. The justification for this was questioned by Hogg (1902, pp. 121–2) when he synonymized *Eucyrtops* with *Aganippe*. Since then *latior* has been retained within *Aganippe*. However, there is now evidence that the species traditionally regarded as belonging to *Aganippe* can be divided into two natural groups, the principal morphological difference being presence or absence of dorsal abdominal sigilla. Those species possessing sigilla are here retained within *Aganippe*, those lacking sigilla are placed in the revived genus *Eucyrtops*.

Pocock (1897, p. 114) described the genus *Anidiops* (type species *manstridgei*) from a single dried female specimen from Lawlers, W.A. The distinctive features of this animal were the non-corrugated abdomen with a “clothing of longish hairs intermixed above with spines . . .” and the anterior lateral eyes situated on the anterior margin of the carapace and separated by “a space which is about equal to their diameter . . .”. Otherwise Pocock comments that the genus is “closely allied to

Idiosoma in the majority of its characters". The "long spines" which Pocock reports present on the abdominal dorsum (p. 116) are here interpreted as being the long bristles characteristic of the median dorsal region of most Aganippini (and which are particularly pronounced in *Gaius hirsutus* Rainbow & Pulleine).

Pocock's description alone would barely suffice to attribute a specimen to the genus, let alone the species *manstridgei*. Fortunately, Hogg (1902, p. 125 and pl. 13, fig. 9) made a further diagnostic note on the specimen. This in essence was as follows: A line drawn between the anterior edges of the posterior lateral eyes (PLE) would pass anterior to the mid line of the anterior median eyes (AME).

The type specimen of Rainbow and Pulleine's species *G. hirsutus* also exhibits this character. This specimen (Australian Museum No. K40896) has pronounced spinules on the labium, maxillae, and sternum. Further reference to Pocock's description of *A. manstridgei* reveals the following statement (p. 114): "*Maxillae, coxae* of legs (especially of first and second pairs), anterior part of sternum, and labium covered thickly with pores elevated on tubercles, indicating the presence of a clothing, unhappily rubbed off, of stout setae, or, perhaps, spines".

From this one can infer the original presence of spinules similar to those noted above in *G. hirsutus*. From near Lawlers, the author has collected *G. hirsutus*. Only two other species of Aganippini are known to occur near Lawlers, these being *G. villosus* Rainbow (whose eye arrangement could not be confused with that of *A. manstridgei*) and *Aganippe raphiduca* Rainbow & Pulleine which in that part of its range has the PLE relatively small so that their anterior edges are not in advance of the mid points of the AME. Thus *G. hirsutus* is to be regarded as a synonym of *A. manstridgei*.

All specimens of *A. manstridgei* (= *G. hirsutus*) and *G. villosus* collected by the author were observed to have in the burrow a structure referred to as a "sock" (Section IV(g), Figs. 23B-23D). This behavioural similarity, which is not shared by any other aganippine, has been taken to imply that the two species are congeneric. Since the name *Anidiops* has priority over *Gaius* the species *G. villosus* Rainbow now becomes *A. villosus* (Rainbow).

Hogg (1902, pp. 131-2) erected the genus *Blakistonia* and since then this genus has been grouped with the aganippine genera (Simon 1903; Rainbow 1914; Rainbow and Pulleine 1918), mainly on account of the eyes which are arranged in 3 rows from the edge of the caput backwards of 2, 2, and 4 eyes (as in the aganippine genera). However, in general features *Blakistonia* appears to have more affinity with the genera *Arbanitis* Koch and *Dyarcyops* Hogg than with the Aganippini.

This affinity is especially marked in the labium of these genera which is elongate rather than broad and is often straight or pointed in front instead of indented. The similar eye arrangement has probably developed convergently in the two groups *Arbanitini* and *Aganippini*.

The present study therefore recognizes four genera as constituting the tribe Aganippini, these being *Idiosoma* Ausserer, *Aganippe* Cambridge, *Eucyrtops* Pocock, and *Anidiops* Pocock; *Gaius* is synonymized with *Anidiops*, and *Blakistonia* is excluded from the tribe.

TABLE 5
LEG SPINATION OF 46 SPECIMENS OF EUCYETOPS RIPARIA

Appendage		No. of Spines																						
No.	Aspect	Segment	Frequency of Occurrence																					
I	Ventral	Tibia	1	5	5	6	9	7	3	4	1	3	5	5	3	6	2	1	1	1	1	1	1	1
		Metatarsus Tarsus			6 35	1 3 1 1		3 2	7 13	7 14	10 9	1												
II	Ventral	Tibia	1	5	5	6	9	7	3															
		Metatarsus Tarsus		2	6	26 10	1 1 1	1 13	10 9	8 3														
III	Ventral	Metatarsus Tarsus		1	4	9	8	9	7	6	1		1											
	Ventral	Tarsus			2	6	15	11	11	1														
	Dorsal	Metatarsus	1	1	1	2	29	11	1															
	Dorsal	Tarsus	7	36	2	1																		
	Pro-latero-dorsal	Patella Tibia	32	6	4 22	8 1	8 1	3	1															
IV	Ventral	Metatarsus Tarsus		1	4	6 11	10	8	3	2	1													
		Tarsus			1	6	7	4	2	4	4	4	1	1	1									
Palp	Ventral	Tibia Tarsus				1	2	1	3	9	11	8	5	3	2	4	2	8	5	4	3	3	2	6

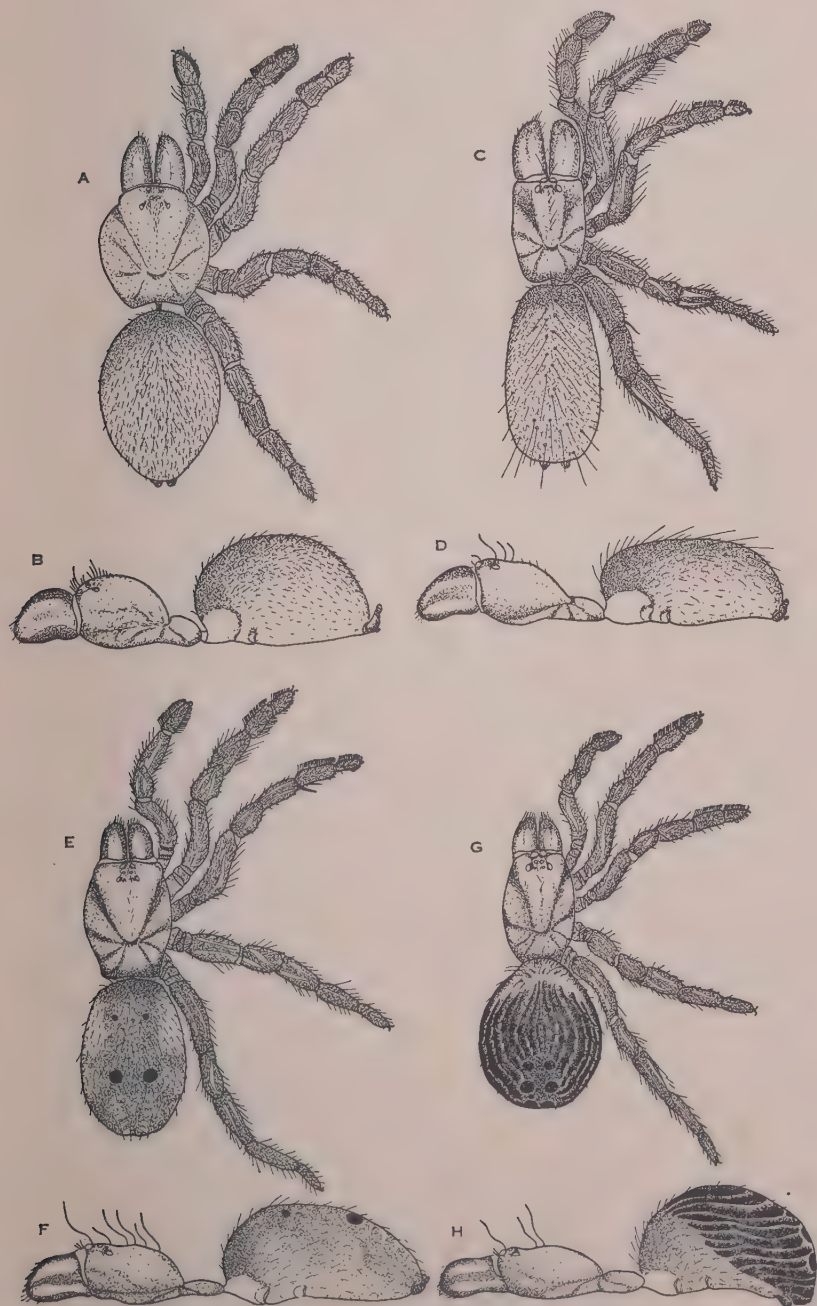


Fig. 2.—Dorsal and profile aspects of a representative of each aganippine genus (female specimens). A, B, *Eucyrtops latior* (Cambridge) (B.M. 52/77); C, D, *Anidiops manstridgei* Pocock (B.M. 54/401); E, F, *Aganippe raphiduca* Rainbow & Pulleine, twig-lining race (B.M. 54/373); G, H, *Idiosoma nigrum* Main (B.M. 53/88). $\times$ c. 2.

TABLE 6
AUSTRALIAN AGANIPINE SPECIES RECORDED IN LITERATURE

Name in Literature	Revised Status	Name in Literature	Revised Status
<i>Aganippe bancrofti</i> Rainbow & Pulleine, 1915	Probably a barychelid	<i>Aganippe smeatoni</i> Hogg, 1902	<i>Aganippe smeatoni</i> Hogg, 1902
<i>Aganippe berlandi</i> Rainbow, 1914	<i>Aganippe smeatoni</i> Hogg, 1902 (?)	<i>Aganippe subtristis</i> Cambridge, 1877	<i>Aganippe subtristis</i> Cambridge, 1877
<i>Aganippe latior</i> Cambridge, 1877	<i>Eucyrtops latior</i> Cambridge 1877	<i>Aganippe tasmanica</i> Hickman, 1927	<i>Arbanitis tasmanica</i> (Hickman), 1927
<i>Aganippe modesta</i> Rainbow & Pulleine, 1915	<i>Aganippe smeatoni</i> Hogg, 1902 (?)	<i>Aganippe villosa</i> Rainbow & Pulleine, 1915	<i>Aganippe smeatoni</i> , Hogg, 1902 (?)
<i>Aganippe occidentalis</i> Hogg, 1903	<i>Aganippe occidentalis</i> Hogg, 1903	<i>Aganippe whitei</i> Rainbow, 1915	<i>Anidiops manstrilgei</i>
<i>Aganippe ornata</i> Rainbow & Pulleine, 1915	<i>Aganippe</i> sp. (?)	<i>Anidiops manstrilgei</i> Pocock, 1897	Pocock, 1897
<i>Aganippe pelychroa</i> Rainbow & Pulleine, 1915	<i>Aganippe smeatoni</i> Hogg, 1902 (?)	<i>Gaius villosus</i> Rainbow, 1914	<i>Anidiops villosus</i> (Rainbow), 1914
<i>Aganippe pulleinei</i> Hogg, 1902	<i>Aganippe subtristis</i> Cam- bridge, 1877 (?)	<i>Gaius hirsutus</i> Rainbow & Pulleine, 1915	<i>Anidiops manstrilgei</i> Pocock, 1897
<i>Aganippe rainboui</i> Pulleine, 1919	<i>Arbanitis</i> sp.	<i>Idiosoma sigillatum</i> (Cambridge), 1870	<i>Idiosoma sigillatum</i> (Cambridge), 1870
<i>Aganippe raphiduca</i> Rainbow & Pulleine, 1918	<i>Aganippe raphiduca</i> Rainbow & Pulleine, 1918	<i>Idiosoma nigrum</i> Main, 1952	<i>Idiosoma nigrum</i> Main, 1952
<i>Aganippe robusta</i> Rainbow & Pulleine, 1918	<i>Aganippe subtristis</i> Cambridge, 1877	<i>Idiosoma hirsutum</i> Main, 1952	<i>Idiosoma sigillatum</i> N.
<i>Aganippe simpsoni</i> Hickman, 1944	<i>Aganippe occidentalis</i> Hogg, 1903 (?)		<i>Aganippe raphiduca</i> (?)

Table 6 lists the recorded species of the genera as they stand at present in the literature. Where such names are not accepted in the present study the revised status is given. Reasons for modification of the old list are discussed in context.

Three new species of Aganippini are here described and including these the present study recognizes three species of *Eucyrtops*, two species each of *Anidiops* and *Idiosoma*, and five species of *Aganippe*. A representative of each genus is illustrated in Figure 2.

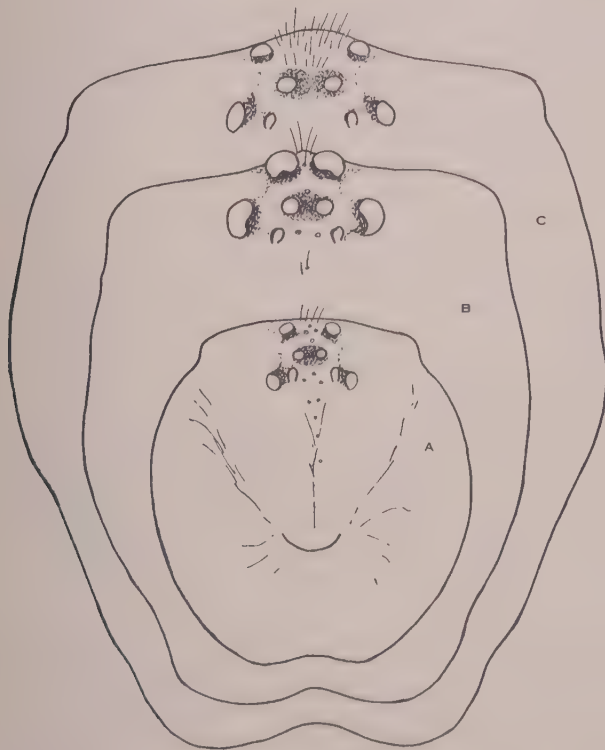


Fig. 3.—Outlines of carapaces of female aganippine specimens.
A, *Eucyrtops riparia*, sp. nov.; *B*, *Anidiops manstridgei* Pocock;
C, *Anidiops villosus* (Rainbow). All to same scale.

(c) *Synopsis of Genera and Species*

With the exception of the holotypes of *Idiosoma nigrum* Main and *I. hirsutum* Main (Main 1952), neither the holotype nor allotype of any of the previously described aganippine species were specifically designated as such in the literature. However, in many species descriptions it was stated that only a single specimen was available, thus by inference such specimens are holotypes and are referred to as such. In the following synopsis some allotypes are herein designated as such.

Genus EUCYRTOPS Pocock

Eucyrtops Pocock, 1897, Ann. Mag. Nat. Hist. (6) **19**: 113. Hogg, 1901, Proc. Zool. Soc. Lond. **1901** (2): 232.

Aganippe Cambridge, 1877 (ad partem *latior*), Ann. Mag. Nat. Hist. (4) **19**: 29, pl. 6, fig. 4. Hogg, 1902 (ad partem *latior*), Proc. Zool. Soc. Lond. **1902** (2): 125, 126, pl. 13, fig. 5. Simon, 1903 (including *Eucyrtops* as synonym), Hist. Nat. Araig., Suppl. Gen., p. 902. Rainbow, 1912 (ad partem *latior*), Rec. Aust. Mus. **9**: 111.

Type species *Aganippe latior* Cambridge, 1877.

Diagnosis.—Differs from *Aganippe* and *Idiosoma* by absence of dorsal abdominal sigilla. Differs from *Anidiops* by absence of a sock in the burrow (see Section IV(g)) and by characteristic shape of carapace, which has a conspicuously broad rounded contour (Figs. 2A, 3A), and in the somewhat globose abdominal outline (Figs. 2A, 2B). The complete absence of twig-lining behaviour* further distinguishes *Eucyrtops* from *Aganippe*, *Anidiops*, and *Idiosoma*.

EUCYRTOPS LATIOR (Cambridge)

Aganippe latior Cambridge, 1877, Ann. Mag. Nat. Hist. (4) **19**: 29, pl. 6, fig. 4. Hogg, 1902, Proc. Zool. Soc. Lond. **1902** (2): 126, pl. 13, fig. 5. Rainbow, 1912, Rec. Aust. Mus. **9**: 111.

Eucyrtops latior Pocock, 1897, Ann. Mag. Nat. Hist. (6) **19**: 113, 114. Hogg, 1901, Proc. Zool. Soc. Lond. **1901** (2): 232.

Diagnosis.—*Female*: Weakly developed spines on the ventral faces of tarsus and tibia of palp, and tarsus, metatarsus, and tibia of legs I and II (Figs. 4A–4C); usually only 1 ventral spine on tibia I and no ventral spines on tibia II (see Table 4). A high caput slopes upwards posteriorly from anterior edge to behind eyes. Generally very dark in colour, almost black, shining, glabrous. Matures with carapace length at 5.00 mm.

Male.—Palpal tibial spines and apophysis and structure of the stigma as in Figures 5C and 5E. Apophysis and weak spines present on tibia I (Fig. 7A). Range in carapace length 4.40–6.70 mm. Colour usually black.

Types.—Holotype female from Perth, collected by G. Clifton (not seen), in the British Museum of Natural History. Allotype male (herein designated and described), Byford, W.A., collected from burrow by the author, 18.iv.1953 (B.M. 53/92, to be deposited in the Western Australian Museum).

* The term "twig-lining" is here used to describe the habit of certain spiders which attach twigs, by their ends, in radial fashion, to the rim of the burrow. These twigs are then used as "feeling lines" while foraging. The habit was first described for the *Aganippini* by Rainbow (1914, pp. 198–9) for *Anidiops villosus*. Rainbow, quoting from correspondence from W. B. Alexander, stated as follows: "The top of the tube projects about a quarter of an inch above the level of the ground, and a series of twigs are incorporated in this portion by their ends. These stand out in radial fashion all round it, on the surface of the ground, and as they are mostly two or three inches long, and some of them are branched, they must have rendered the nest very conspicuous". However, Rainbow did not ascribe any function to the twigs. The function of the twigs as an adjunct to feeding was first mentioned by Main (1957). Burrows with attached twig lines are illustrated in Plates 1 (Fig. 4), 3, 4, 5, and 6 (Figs. 1 and 2).

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA*: Quindanning, 12 miles W. of, Harvey–Quindanning Rd., 1; Crossman, 5 miles E. of, 2; Dwellingup, 2 miles N. of, 1; Bushmead, 1; Bullsbrook, E. of, on scarp, 1; Toodyay, 6 miles W. of, Redhill Rd., 2; Bolgart, 1; Bolgart, 3 miles SE. of, 1; Bolgart, 9.5 miles SW. of, 1; Botherling, 2; Goomalling, 1; the Wongan Hills, 3; New Norcia, 3 miles E. of, 4; Carani, 1.5 miles E. of, 2; Kadji Gate, 1; Mt. Magnet, 30 miles E. of, 1; Dinninup, 1; Albany Highway, 85–86 mile peg, 1; Albany Highway, 153 mile peg, 4; Albany Highway, 164 mile peg, 8; Katanning, 6 miles N. of, 1; Broomehill, 4; Pallinup R., Borden–Chester Pass Rd., 2; Borden, 1 mile S. of, 2; Red Gum Pass (Stirling Ranges), 7 miles N. of, 1; Cranbrook, 1; Lake Grace, 6 miles N. of, 7; Hyden, 2.5 miles NE. of, 3; “The Humps”, Hyden, 2; Jilakin Rock, 4 miles N. of, 1; Newdegate, 1 mile E. of, 4; Lake King, 3 miles W. of, 1; Ravensthorpe, 7 miles S. of, 2; Peak Charles, 1; Peak Charles, 5 miles N. of, 1; Yellowdine, 5 miles W. of, 1; Higginsville, 9 miles N. of, 2; Pioneer, 1; Norseman, 15 miles N. of, 1; Norseman, a few miles S. of, 1; Norseman, 9 miles NE. of, 1; Daniell, 4 miles S. of, 1; Norseman, 66 miles E. of (Eyre Highway), 1; Norseman, 68 miles E. of (Eyre Highway), 1; Fraser Range (Eyre Highway), 4; Magooinya Rock (Balladonia), 1; Emu Rock (Nanambinia), 3; Booanya Rock, 12 miles S. of, 4; Pine Hill (Balladonia–Israelite Bay track), 3; Israelite Bay, 11 miles N. of, 1; Balladonia, 20 miles W. of, 1; Balladonia, 9 miles E. of, 1; Balladonia, 60 miles E. of, 1.

Males.—WESTERN AUSTRALIA: Byford, 1 (allotype); Jilakin Rock, 5.5 miles N. of, 1; Albany Highway, 164 mile peg, 2.

Specimens with everted fovea: females or immature specimens.—WESTERN AUSTRALIA: Albany Highway, 112 mile peg, 4.

Remarks.—Cambridge made the specific description from a single dried female specimen. Until now this was the only known specimen of the species. The abdomen of Cambridge's specimen was shrivelled and no diagnostic abdominal characters were noted. The absence of sigilla is assumed, since from the author's collecting, it is apparent that all aganippines coming from south-western Western Australia and having an eye arrangement like that figured by Cambridge for his *A. latior* (Cambridge (1877) pl. 6, fig. 4) lack dorsal abdominal sigilla.

This species occurs in situations of dense spatulate leaf litter, such as is formed by eucalypts, sometimes under a dense mat of *Casuarina* litter. The fragile door of the burrow is made of soil and litter fragments and opens below or amongst the litter. Food consists almost entirely of beetles.

Four female specimens of what are probably aberrant specimens of *latior* have been collected. These animals have a strongly everted fovea as illustrated in Figure 6. They are otherwise essentially like *latior*, except that some specimens have the anterior spines (on palp and on legs I and II) more pronounced than does *latior*. All these specimens were collected from the one locality and the burrows were within

* The Western Australian localities may be found by reference to the Western Australian Department of Lands and Surveys Topographical Series of Maps, Sheets 1–8 inclusive, 1946. Scale 1 in. = 10 miles. South Australian localities may be found by reference to “Gregory's Road Map of South Australia.” Scale 1 in. = 16 miles. (Gregory's Guides and Maps: Sydney.) Some localities along the Eyre Highway (W.A. and S.A.) not included in the above are indicated on the Shell Road Map, Adelaide to Perth. Scales: South Australia, 1 in. = 8 miles; Western Australia, 1 in. = 10 miles. The specimens in these lists refer only to those in the author's collection.

a few yards of one another. The ecological situation was typical of a *laticornis* habitat (amongst dense litter). The burrows opened above the litter surface but contained beetle remains.

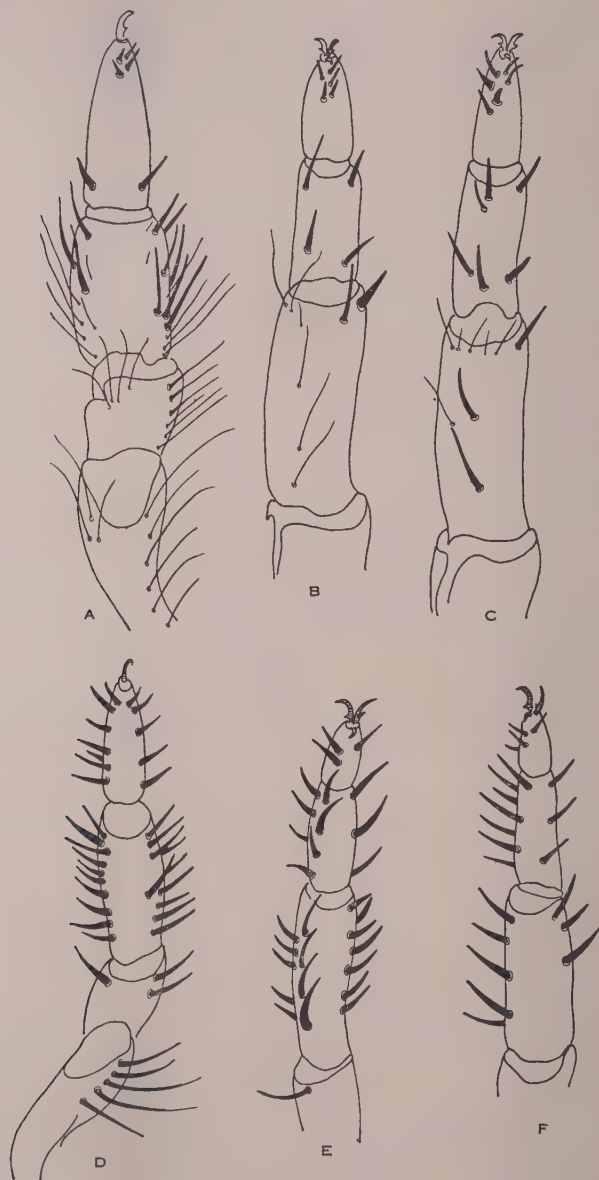


Fig. 4.—Ventral spines of palp and legs I and II of *Eucyrtops* Pocock. A, B, C, right palp, leg I, and leg II respectively of *E. laticornis* (Cambridge) (B.M. 52/77); D, E, F, right palp, leg I, and leg II respectively of *E. riparia*, sp. nov. (B.M. 54/127).

EUCYRTOPS RIPARIA, sp. nov.

Diagnosis.—*Female*: Heavily developed spines on ventral faces of tarsus and tibia of palp and tarsus, metatarsus, and tibia of legs I and II (Figs. 4*D*–4*F* and Table 5). Caput does not slope up posteriorly from front margin. The abdomen of

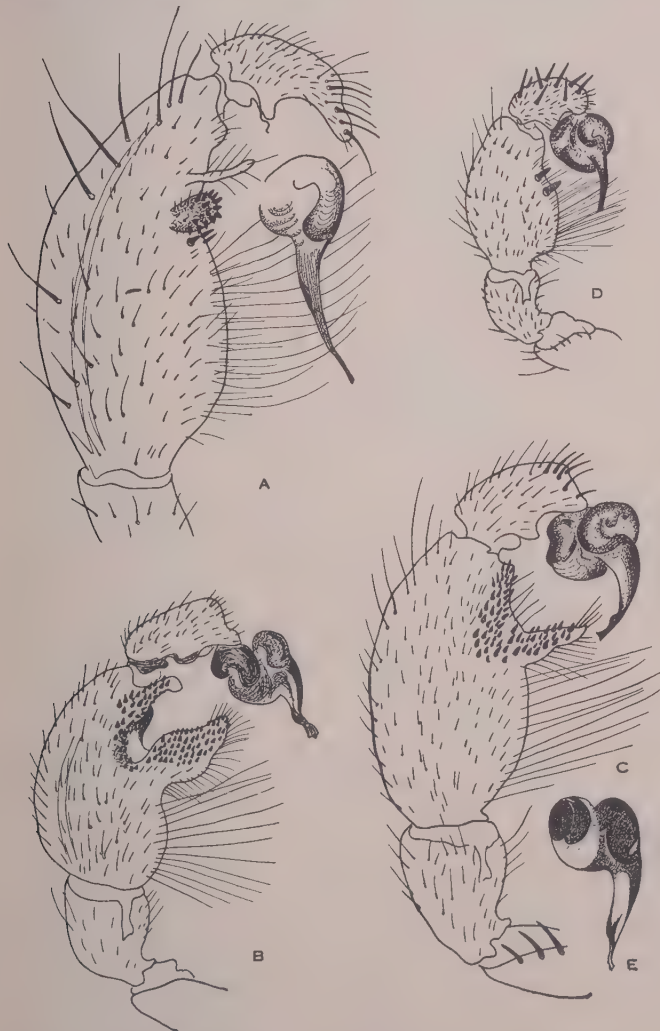


Fig. 5.—Retrolateral aspects of right palps of male aganippines. *A*, *Anidiops manstridgei* Pocock (allotype); *B*, *An. villosus* (Rainbow) (allotype); *C*, *E* (stigma from slightly more ventral angle), *Eucyrtops latior* (Cambridge) (allotype); *D*, *E. riparia*, sp. nov. (B.M. 53/132).

specimens from the Stirling Ranges usually has a distinct pattern of pale lateral patches on either side of the mid-dorsal region. A single aberrant specimen with everted fovea has been collected.

Male.—Differs from other species of *Eucyrtops* by: stout spines on dorsum of palpal tarsus, presence of heavy spines on ventral faces of legs I and II (Fig. 7B), absence of spines and apophysis on palpal tibia (Fig. 8A), and absence of apophysis on tibia I (Fig. 7B) (specimens from type locality). The male parts of specimens from the Stirling Ranges are very similar to those of *latior* specimens. They lack heavy leg spination but have the typical spined apophysis on tibia I and a spined process on the palpal tibia. The region between this process and the apical end of the segment has fewer of the stubby spines than does *latior* and the stigma lacks the small flange near the tip, presence of which is characteristic for *latior* (Figs. 8D-8E). A northern specimen from Ebano Creek has several stout spines on the palpal tibia as shown in Figure 5D.

Range in carapace length of specimens collected is 4.20-5.50 mm.



Fig. 6.—Profile view of carapace of specimen of *Eucyrtops latior* (Cambridge) showing everted fovea (B.M. 53/252).

Types.—Holotype female and allotype male (herein designated and described) from 1 mile W. of Mt. Misery (Moora) collected from burrows by the author. Holotype, 26.v. 1954 (B.M. 54/102), allotype, 5.v. 1956 (B.M. 56/225). (To be deposited in the Western Australian Museum.)

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Stirling Range, Moingup Spring, 71; Stirling Range, Bluff Knoll, 3; Crambrook 1; Balingup, 2; Guildford, 8; Toodyay, 6 miles W. of, Red Hill Rd., 1; Bullsbrook, 7 miles E. of, Chittering Valley Rd., 2; Wannamal, 7 miles S. of, 1; Mt. Misery, 1 mile S. of (W. of Moora), 39 (includes holotype); Mt. Misery (W. of Moora), 2; Munbinea Creek, near junction with Hill R., 3; junction of Munbinea Creek and Hill R., 1 mile E. of, 1; Donkey Creek, headwaters of (W. of Arrino), 1; Ebano Creek (E. of Mingenew), 9; Woolaga Creek (E. of Mingenew), 1; Koolanooka Hills, 23; Morawa, 1 mile S. of, 5; Canna, 3; Northampton, 3; Kirkalocka, 6 miles N. of homestead, 14; Lawlers, 5 miles N. of, 1.

Males.—WESTERN AUSTRALIA: Stirling Range, Moingup Spring, 2; Ebano Creek, 1; Mt. Misery, 1 mile S. of (W. of Moora), 6 (includes allotype).

Aberrant specimens: females or immature specimens (with grossly enlarged and approximated eyes but lacking maxillary spinules). WESTERN AUSTRALIA: Madura Pass, 15 miles E. of, 1; Eucla, 22 miles W. of, 1; Eucla, N. of, on scarp, 1.

Remarks.—Complete reproductive isolation between *riparia* specimens from the Stirling Range and *latior* may not exist. However, due to the general behavioural and morphological (females) differences, the two are at present considered specifically distinct.

The species occurs characteristically in riparian situations where it makes a stiff, flap-like soil door (Plate 1, Fig. 1).



Fig. 7.— *A*, *Eucyrtops latior* (Cambridge), ventral aspect of right leg I, showing tibial apophysis (allotype); *B*, *E. riparia*, sp. nov., ventral aspect of right leg I showing heavy spination and absence of any apophysis (B.M. 53/132); *C*, *Aganippe subtristis* Cambridge, retrolateral aspect of right pedipalp of male specimen (allotype); *D*, *Ag. raphiduca* Rainbow & Pulleine, type race, tip of stigma of right palp, retrolateral aspect (B.M. 53/276); *E*, *Idiosoma* Ausserer, tip of stigma of right palp, retrolateral aspect. *F*, *Ag. cupulifer*, sp. nov., tip of stigma of right palp, retrolateral aspect.

EUCYRTOPS EREMAEA, sp. nov.

Diagnosis.—*Female*: Differs from *riparia* by absence of heavy spination on palps and anterior legs. Very similar to *latior*, having a high sloping caput and glabrous carapace; differs in colour and size. In life, animal is light brownish in colour with darker transverse markings on abdominal dorsum, whereas *latior* is a uniform dark brown, almost black. Species matures at 3.70 mm whereas the smallest reproductively active *latior* specimen known is 5.00 mm.

Male.—Differs from *riparia* and *laticornis* in its much smaller size (see Table 2). Colour in life generally light yellowish brown with darker smudges at base of legs

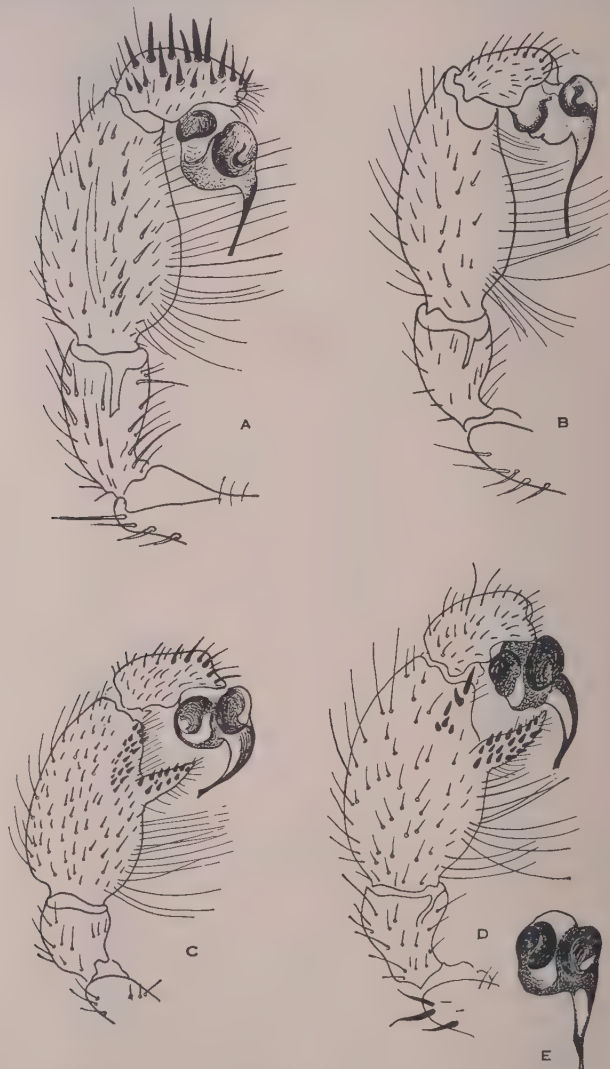


Fig. 8.—Retrolateral aspect of right pedipalps of male specimens of *Eucyrtops*. A, *E. riparia*, sp. nov. (allotype); B, *Eucyrtops* "spinular" form (B.M. 56/247); C, *E. eremaea*, sp. nov. (holotype). D, E (stigma from more ventral angle), *E. riparia*, sp. nov. (Stirling Range specimen) (B.M. 56/115).

and around eyes, dorsum of abdomen with dark brown anterior smudge followed by dark brown transverse bands (other species darker and more uniform colour). Palp structure similar to that of *laticornis* except there are fewer spines in area between

tibial apophysis and apical region of tibia and the stigma lacks the slight terminal flange present in *latior* (see Fig. 8C). Apophysis and weak spines present on tibia I, as in *latior*.

Types.—Holotype male and allotype female (herein designated and described) from Cardinia Creek (E. of Malcolm), W. A., collected by A. R. Main from burrows, 21.v.1956. Holotype (B.M. 56/353) and allotype (B.M. 56/375) to be deposited in the Western Australian Museum.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Cardinia Creek, about 4.5 miles E. of Malcolm, 23 (includes allotype); Laverton, 2 miles W. of, 9.

Males.—WESTERN AUSTRALIA: Cardinia Creek, 6 (includes holotype).

Remarks.—The species has only been found along the low banks of braided creeks in the mulga (*Acacia aneura* F. Muell.) country of Western Australia. The burrows occur under a dense mat of *Acacia* litter which may obscure the soil. The doors are made of soil and are relatively thick and cork-like, and open beneath the litter. The occurrence in such a habitat distinguishes the species from both *latior* and *riparia*.

INCERTAE SEDIS

Genus EUCYRTOPS Pocock

(a) Seventeen female specimens and one male specimen of a distinct biological form. Resembles *riparia* by having numerous heavy spines on the ventral faces of the palp, and tarsus, metatarsus, and tibia of the two anterior pairs of legs. Usually has relatively enlarged eyes; in fact in some specimens the ALE are so enlarged and approximated as to resemble the *Idiosoma* extreme (Fig. 25). Differs from the named species of *Eucyrtops* by always having well-developed maxillary spinules (for structural difference between cuspules and spinules see Figs. 10B, 10C).

These specimens have been collected from widely separated localities within the geographical range of *latior* and occasionally *riparia* but always from a litter habitat. The burrows differ from those of *latior* by having the door opening above the litter layer instead of within it.

One male specimen has been collected from Gillingarra. In general features it closely resembles *riparia* except that it lacks the spines on the palpal tarsus (Fig. 8B) and also lacks the heavy leg spines characteristic of *riparia*. Like the northern specimens of *riparia* it has no apophysis on the first tibia (Fig. 9A). The shape of the stigma is similar to that of *riparia* (Figs. 8A, 8B). Specific status of this form is still indefinite and until more biological data are available the form will be referred to as *Eucyrtops* "spinular" form.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Gillingarra, 2 miles N. of, 1; Gillingarra, 7; Mogumber, 1; Wannamal, 7 miles S. of, 1; Cullalla, 4; Dwarda, 1; Albany Highway, 112 mile peg, 1; Juranda Rock, 1.

Males.—WESTERN AUSTRALIA: Gillingarra, 1.

(b) Three female specimens from burrows in bare litterless ground. The upper part of the burrow ran for 2 or 3 in. horizontally just beneath the soil surface, before

bending and continuing vertically. The soil doors were fragile and flap-like. All specimens have relatively heavy anterior spination like *riparia*; one specimen has a slight spinular development on the maxillae. The general facies of the animals is that of *riparia* rather than *laticor* or *cremacea* but the situation in which they were found, the burrow structure, and the localities precludes the specimens being typical of any of these three species.

Specimens examined

Females or immature specimens.—WESTERN AUSTRALIA: Wurarga, 4 miles E. of, 1; Pindar, 5 miles E. of, 2.



Fig. 9.—A, *Eucyrtops* "spinular" form, ventral view of right leg I of male specimen (B.M. 56/247) showing absence of apophysis and heavy spines; B, *Aganippe cupulifer*, sp. nov., ventral view of apical end of left leg I, male specimen, twig-lining form (B.M. 56/272); C, *Aganippe* "Walebing" race, ventral view of apical end of right leg I, male specimen (B.M. 55/117).

Genus ANIDIOPS Pocock

- Anidiops* Pocock, 1897, Ann. Mag. Nat. Hist. (6) 19: 114. Hogg, 1901, Proc. Zool. Soc. Lond. 1901 (2): 231-2; 1902, op. cit. 1902 (2): 125, pl. 13, fig. 9. Simon, 1903, Hist. Nat. Araig., Suppl. Gen., pp. 901-3, fig. 1052. Rainbow, 1912, Rec. Aust. Mus. 9: 112; Rainbow and Pulleine, 1918, op. cit. 12: 101-2, pl. 21, figs. 52-54.
Genus Rainbow, 1914, Rec. Aust. Mus. 10: 195-9, figs. 6-8. Rainbow and Pulleine, 1918, op. cit. 12: 102-3, pl. 21, fig. 55.

Type species *Anidiops manstridgei* Pocock.

Diagnosis.—Distinguished from *Apantlope* and *Idiosoma* by absence of dorsal abdominal sigilla; differs from *Eucyrtops* by presence of seta in the furrow (see Section IV (g)) and by carapace not having such a broadly rounded contour (Fig.

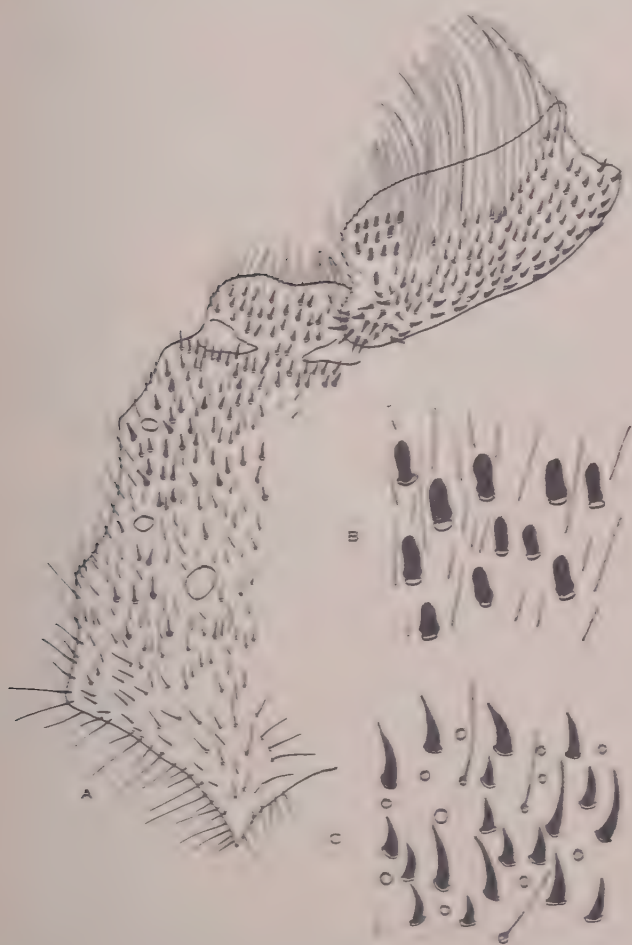


Fig. 10.—*Anidiops manstridgei* Pocock. A, sternum, labium, and left maxilla, showing spinules and cuspules (B.M. 54 401); B, enlargement of cuspules; C, enlargement of spinules.

2C, 3B, 3C), by the elongated, straight-sided abdomen (Figs 10C, 15A). This shape may be distorted by development of eggs. Both species of *Anidiops* are twig-dwelling over at least a part of their range; this habit provides another difference from the genus *Eucyrtops*.

ANIDIOPS MANSTRIDGEI Pocock

Anidiops manstridgei Pocock, 1897, Ann. Mag. Nat. Hist. (6) 19: 114. Hogg, 1901, Proc. Zool. Soc. Lond. 1901 (2): 231-2. Simon, 1903, Hist. Nat. Araig., Suppl. Gen., p. 901-3, fig. 1052. Rainbow, 1912, Rec. Aust. Mus. 9: 112. Rainbow and Pulleine, 1918, op. cit. 12: 101-2, pl. 21, figs. 52-54.

Aganippe whitei Rainbow, 1915, Trans. Roy. Soc. S. Aust. 39: 774-5, pl. 67, figs. 1 and 2. *Gaius hirsutus* Rainbow and Pulleine, 1918, Rec. Aust. Mus. 12: 102-3, pl. 21, fig. 55.

Diagnosis.—*Female*: Heavy spinules on labium, maxillae, sternum, and occasionally on leg coxae as well (Figs. 10A and 10C); extraordinarily enlarged eyes, usually with anterior edges of the PLE in advance of the mid points of the AME (subject to some degree of variation since in some specimens, mainly those from Eyre Peninsula, S.A., the eyes are not enlarged to this extent (see Fig. 25)).

Male.—Apophyses of palpal tibia like the "*Aganippe-Idiosoma*" type, i.e. an upper, thin, digital process and a lower, spinous, burr-like process; stigma of palp long, pointed, and almost straight (Fig. 5A), eyes as in female.

Types.—Holotype female from Lawlers, W.A., collected by W. O. Mansbridge (misspelt Manstridge by Pocock), in the British Museum of Natural History (not seen). Allotype male (described by Rainbow and Pulleine 1918), Mallala, S.A., collected by T. Nevin, 10.v.1910, in the Australian Museum, No. K40874 (seen).

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Lawlers, 6 miles W. of, 1; Leonora, 17 miles NW. of, 1; Stoneville, about 3 miles E. of, 1; Emu Rock, 5 miles S. of (about 40 miles S. of Coolgardie), 1; Norseman, 15 miles N. of, 1; Fraser Range, 78 mile peg, Eyre Highway, 1; Magooinya Rock (Balladonia), 5; Balladonia, 3; Emu Rock (Nanambinia), 1; Balladonia, 43 miles E. of, 1; Cocklebidly Tank, 8; Moonera Tank, 5 miles E. of, 1; Eucla, 22 miles W. of, 2. SOUTH AUSTRALIA: Albalá-Karoo Tank, 2; Yangoonabbie Tank, 2 miles E. of, 1; Gundalabbie Tank, 4 miles E. of, 2; Ivy Tanks, 14 miles E. of, 6; Colona, 9 miles E. of, 4; Colona, 13 miles E. of, 3; fork of E. and W. tracks to Fowler's Bay, S. of Eyre Highway, 1; Penong, 11 miles W. of, 2; Penong, 10 miles E. of, 1; Streaky Bay, 1; between Port Kenny and Streaky Bay, 2; Tallala Tank, 6 miles E. of, 1; Wirrulla, 10 miles W. of, 2 (twig-lining); Karcultaby, 1 mile E. of, 1 (twig-lining); Waddikee, 2 miles W. of, 1 (twig-lining); Koonibba, 3 miles SE. of, 1; Thurlga, 14 miles E. of, 1; Coultá, 4 miles S. of, 3; Elliston, 1; Lock, 18 miles W. of, 1; Cummins, 6 miles N. of, 1; Cummins, 8 miles E. of, 6; hills E. of Cummins, 2; Arno Bay, 15 miles S. of, 1; Cowell, 10 miles S. of, 2; Farina, 1; Leigh Creek, 3; between Hawker and Wilpena Pound, 1; Dublin, 3; Clare, 15 miles N. of, 1.

Remarks.—*Aganippe whitei* Rainbow, the type of which the author has seen in the South Australian Museum, is readily recognizable as *Anidiops manstridgei* by the following points: it lacks dorsal abdominal sigilla, has heavy spinules on labium, maxillae, and sternum, and has the PLE so enlarged that they extend anterior to the mid points of the AME.

ANIDIOPS VILLOSUS (Rainbow)

Gaius villosus Rainbow, 1914, Rec. Aust. Mus. 10: 195-9, figs. 6-8.

Diagnosis.—*Female*: No spinules on labium, sternum, leg coxae, and sometimes absent from maxillae; eyes never enlarged to the same extent as in *A. manstridgei*, and anterior edges of PLE never extending anterior to mid points of AME (Fig. 25).

Male.—Apophysis of palpal tibia consisting of a large, apically "hooked", and spiny upper process and lower, also large, pointed and very spiny process; stigma relatively short and with blunt tip (Fig. 5B); eyes as in female.

Types.—Holotype female from Minnivale, W.A., collected by J. P. Harris, in the Australian Museum, No. K34393 (seen). Allotype male (herein designated and described) from Dowerin, W.A., collected by D. Jones, in the Western Australian Museum, No. 40-203.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Thomas R. (Esperance Plains), 7; Salmon Gums, 6 miles S. of, 1; Salmon Gums, 5 miles N. of, 1; Peak Charles, 6; Lake King-Dowak track, 9 miles E. of, 90 Mile Tank, 2; Higginsville, 6 miles S. of, 1; Boorabbin, 1; Minnivale, 2; Nungarin, 10 miles N. of, 1; Ballidu, 18 miles E. of, 3; Morawa, 1; Lakeswood, 1; Lakewood, 6 miles E. of, 1; Golden Ridge, 10 miles E. of, 1; Bulong, 10 miles W. of, 2; Broad Arrow, 20 miles N. of, 13; Menzies, 4 miles N. of, 1; Jessop Well, 1; Cullewa, 2 miles S. of, 2; Great Northern Highway, 5 miles N. of Mt. Gibson turnoff, 2; Paynes Find, 13 miles W. of, 5; Mt. Magnet, 30 miles E. of, 1; north-west coastal highway, 23 miles N. of Murchison R., 1; north-west coastal highway, 19 miles N. of Murchison R., 1; Beatty, 2; Pindar, 5 miles E. of, 1; Leonora, 17 miles NW. of, 3; Poison Creek, 5 miles SE. of, 3; Lawlers, 3 miles S. of, 1; depot Spring Stn., about 5 miles E. of, 2; Blackhill Stn. about 8 miles E. of, 3.

Males.—WESTERN AUSTRALIA: Tambellup, 2; Wyalkatchem, 1; Koorda, 1.

Genus AGANIPPE Cambridge

Aganippe Cambridge, 1877 (ad partem *subtristis*), Ann. Mag. Nat. Hist. (4) 19: 28–9, pl. 6, fig. 3. Simon, 1892, Hist. Nat. Araig. 1: 102, 103, and 106, fig. 104; 1903, op. cit., Suppl. Gen., pp. 901–3, fig. 1050. Pocock, 1897, Ann. Mag. Nat. Hist. (6) 19: 112–13. Hogg, 1901, Proc. Zool. Soc. Lond. 1901 (2): 229, 231; 1902, op. cit. 1902 (2): 125–30, pl. 13, figs. 3, 4, 6, 7, text-figs. 23, 24. Rainbow, 1912, Rec. Aust. Mus. 9: 111, 1914, op. cit. 10: 199–202, text-figs. 9–13. Rainbow and Pulleine, 1918, Rec. Aust. Mus. 12: 89–101, pl. 12, fig. 3, pl. 13, figs. 4, 5, pl. 21, figs. 32, 35–51.

Type species *Aganippe subtristis* Cambridge, 1877.

Diagnosis.—Differs from *Eucyrtops* and *Anidiops* by having dorsal abdominal sigilla (Figs. 2E, 2F). Differs from *Idiosoma* by having no abdominal corrugations and usually only 2 pairs of dorsal abdominal sigilla (which are homologous with the 2 anterior pairs of *Idiosoma*). Male palp lacks spines on upper digital apophysis of tibia (except some specimens of *A. raphiduca*).

Several species previously thought to belong to *Aganippe* must be excluded from this genus, as discussed below:

A. tasmanica Hickman (Hickman 1927), which has a relatively long labium and the eyes arranged in 2 rows of 4, is therefore not an aganippine but a species of *Arbanitis*. Professor Hickman has already acknowledged (in litt.) that this species does not belong in the genus *Aganippe* and he kindly forwarded a specimen to the author for examination and comparison.

Of *A. rainbowi* Pulleine, Pulleine (1919, pp. 74–5) states that the front row of eyes is "very slightly recurved" and that the labium is "... beset with about 20 black spines in its central area". Aganippines have the anterior row of eyes strongly procurved, the AME being set well behind the ALE, forming a separate line, and these spiders never possess spines (=cuspules) on the labium. The above

species probably belongs to the genus *Arbanitis*. *A. bancrofti* Rainbow & Pulleine does not belong in the genus *Aganippe* since Rainbow and Pulleine (1918, p. 95) state of the chelicerae: "outer ridge of the furrow of each falx unarmed with teeth, whilst the inner has a row of eight strong teeth". Aganippines always have a row of teeth on the outer margin of the falx as well as on the inner margin. This species is probably a barychelid.

The status of *A. ornata* (described by Rainbow and Pulleine 1918) cannot be ascertained from the literature and the type cannot now be located in the Australian Museum where it was deposited. Until such time as a specimen with biological information can be obtained from the type locality (Eidsvold, Qld.) the name cannot be attributed to any known species.

Female and immature specimens of species of *Aganippe* are morphologically similar and the first clue to their identity was the observation that different populations constructed distinctly different types of door. Later it was found that, generally, distinct male forms were associated with the different door types.

There are five biologically distinct populations known. In the present study these species are referred to under the following names: *A. subtristis* Cambridge, *A. smeatoni* Hogg, *A. occidentalis* Hogg, *A. raphiduca* Rainbow & Pulleine, and *A. cupulifex*, sp. nov.

AGANIPPE SUBTRISTIS Cambridge

Aganippe subtristis Cambridge, 1877, Ann. Mag. Nat. Hist. (4) **19**: 28-9, pl. 6, fig. 3. Simon, 1892, Hist. Nat. Araig. **1**: 106, fig. 104; 1903, op. cit., Suppl. Gen., p. 901, fig. 1050. Pocock, 1895, Ann. Mag. Nat. Hist. (6) **16**: 223; 1897, op. cit. (6) **19**: 112-13. Hogg, 1901, Proc. Zool. Soc. Lond. **1901** (2): 231; 1902, op. cit. **1902** (2): 121, 126, pl. 13, fig. 6. Rainbow, 1912, Rec. Aust. Mus. **9**: 111. Rainbow and Pulleine, 1918, op. cit. **12**: 89, 91-2, pl. 12, figs. 32, 35-37.

Aganippe pulleinei Hogg, 1902, Proc. Zool. Soc. Lond. **1902** (2): 128-30, pl. 13, figs. 3, 4, text-figs. 24 a, b, c. Rainbow, 1912, Rec. Aust. Mus. **9**: 111.

Aganippe robusta Rainbow and Pulleine, 1918, Rec. Aust. Mus. **12**: 97-8, pl. 21, figs. 45, 46.

Diagnosis.—*Female*: With small widely spaced eyes as in Figure 25. No other species of *Aganippe* has such an eye arrangement. Some forms may have the eyes relatively enlarged and closer together (e.g. the Eyre Peninsula population).

Male.—With stigma of palp long, pointed, and slightly bent (Fig. 7C). The dorsum of the palpal tarsus with a cluster of short, stout spines (Fig. 7C). If spines are present on the tarsus in other species they are very few and much longer and tapering.

Two female specimens from Eyre Peninsula at present tentatively included in *subtristis* were observed to have spinose abdomens, similar to the condition found in many of the specimens of *A. raphiduca*.

Types.—Holotype female from Adelaide, in the British Museum of Natural History (not seen). Allotype male (described by Rainbow and Pulleine 1918) from Booboorowie, S.A., collected May 1908, presumably by R. Pulleine, in the Australian Museum, No. K40835 (seen).

Specimens examined

Females and immature specimens.—SOUTH AUSTRALIA: Between Gladstone and Murray-town, 1; Mt. Remarkable, 3; Pichi Richi Pass, 13; Woolshed Flat, 4.

Males.—NORTHERN TERRITORY: Ayers Rock, 1.

A. subtristis (?) (from Eyre Peninsula)

Females and immature specimens.—SOUTH AUSTRALIA: Tumby Bay, 7 miles N. of, 1; mouth of Todd R., 4; White Flat, 5; Yalunda Flat, 1; Cummins, 8 miles E. of, 2; Cummins, 6 miles N. of, 1; Coultla, 4 miles S. of, 1; "Coomunga Springs", 5 miles W. of Port Lincoln, 5; Mt. Drummond, 3 miles S. of, 1; Thistle I., 1.

Remarks.—Cambridge (1877) described this species from a dried female specimen. The description was brief but a clear figure of the eye arrangement, and the locality stated as Adelaide enable an accurate identification of the species. It has been noticed that all female specimens of *Aganippe* coming from Adelaide and north along the Flinders Range, which have a widely spaced eye arrangement as figured by Cambridge (1877, pl. 6, fig. 3) for *A. subtristis* (see Fig. 25), also have dorsal abdominal sigilla; thus the possession of such sigilla by the type of the species can be assumed. In 1918 Rainbow and Pulleine described a male specimen of this species.

A. pulleinei is tentatively synonymized with *subtristis*. Hogg (1902, p. 129) states the stigma of *pulleinei* to be "twisted, but not so much as in *A. smeatoni*" which implies similarity with the stigma of *subtristis* as does also the figure given by Hogg (1902, text-fig. 24a). Secondly, the eyes of *pulleinei* are stated by Hogg to be more or less widespread, the ALE being "two of their diameters apart" (Hogg 1902, p. 129) and the figures given (Hogg 1902, pl. 13, figs. 3 and 4) certainly indicate the arrangement characteristic for *subtristis*. Similarly, the widespread eyes of *robusta* suggest that this form is synonymous with *subtristis*.

AGANIPPE SMEATONI Hogg

Aganippe smeatoni Hogg, 1902, Proc. Zool. Soc. Lond. **1902** (2): 126-7, pl. 13, fig. 7, text-figs. 23a, b, c. Simon, 1903, Hist. Nat. Araig., Suppl. Gen., p. 903, figs. 1054, 1055.

Rainbow, 1912, Rec. Aust. Mus. **9**: 112. Rainbow and Pulleine, 1918, op. cit. **12**: 90.

? *Aganippe berlandi* Rainbow, 1914, Rec. Aust. Mus. **10**: 199-202, figs. 9-13.

? *Aganippe villosa* Rainbow and Pulleine, 1918, Rec. Aust. Mus. **12**: 96-7, pl. 21, fig. 44.

? *Aganippe modesta* Rainbow and Pulleine, 1918, op. cit. **12**: 98-9, pl. 13, figs. 4, 5; pl. 21, figs. 47, 48.

? *Aganippe pelochroa* Rainbow and Pulleine, 1918, op. cit. **12**: 100-1, pl. 21, fig. 51.

Diagnosis.—*Female*: Morphologically indistinguishable from the females of other *Aganippe* species except *subtristis*. The species does not occur in Western Australia and overlaps in range only *subtristis*.

Male.—Differs from the other species of *Aganippe* by having a strongly cork-screw-like twisted palpal stigma, which is "twisted like a ram's horn" (Hogg 1902, p. 127). *A. subtristis* also has the stigma slightly twisted but never to same extent as *smeatoni*; also *smeatoni* lacks the group of stout spines on the palpal tarsus, which is characteristically present in *subtristis*.

The species occurs in riparian situations and builds a slightly inset flap-like door of soil particles.

Types.—Male from Blakiston (?), S.A., collected by T. D. Smeaton, in the British Museum of Natural History (not seen). Allotype female (herein designated and described) from the Myponga turnoff on Willunga Hill, S.A., collected from burrow by the author, 18.xii.1954 (B.M. 54/540), to be deposited in the Western Australian Museum. Door of allotype also to be deposited in the Western Australian Museum.

Specimens examined

Females and immature specimens.—SOUTH AUSTRALIA: Willunga Hill, Myponga turnoff, 1 (allotype); Mt. Lofty, near ridge, 1; Aldgate, 4.

Remarks.—Hogg actually had access to four male specimens which he believed to have come from Blakiston, since they were collected by a Mr. T. D. Smeaton of Blakiston. The distinctive features of the species, emphasized by Hogg were: the ALE one diameter apart and stigma of the palp “rather long and twisted like



Fig. 11.—Retrolateral aspect of left palps of male aganippine specimens: A, *Aganippe smeatoni* Hogg (from Hogg 1902); B, *Ag. occidentalis* Hogg (from Hogg 1903).

a ram's horn" (Hogg 1902, p. 127, text-fig. 23). Hogg's figure of the stigma is reproduced in Figure 11A. Of the apophyses on the palpal tibia Hogg (loc. cit.) stated the following: "On the tibial joint is a double apophysis thickly covered on the outside with short, tapering three-sided spines." Hogg does not make clear, however, whether both the upper and lower parts of the apophysis had these spines. Absence of spines on the upper digital apophysis of *smeatoni* is deduced from the fact that three specimens in the South Australian Museum, which are believed to be three of the four specimens examined by Hogg, lack such spines. Otherwise they agree with Hogg's description and figures.

A. villosa (Bridgewater, S.A.), *A. modesta* (Black Hill, Mt. Lofty, S.A.), and *A. pelochroa* (Mt. Lofty, S.A.), all described from female specimens, the types of which are now not available, are tentatively synonymized with *A. smeatoni*, since it appears from field collecting that there is only one biological population of *Aganippe*, apart from *subtristis*, in the Mt. Lofty Ranges. Rainbow's figure of the

palpal stigma of *A. berlandi* (Rainbow 1914, fig. 11), indicates a corkscrew-like twist, characteristic of *A. smeatoni*. *A. berlandi* is thus tentatively regarded as synonymous with *smeatoni*.

AGANIPPE OCCIDENTALIS Hogg

Aganippe occidentalis Hogg, 1903, Ann. Mag. Nat. Hist. (7) 11: 309–10, figs.

? *Aganippe simpsoni* Hickman, 1944, Trans. Roy. Soc. S. Aust. 68: 22–3, pl. 1, figs. 7–10.

Diagnosis.—*Female*: Morphologically indistinguishable from some forms of *smeatoni*, *raphiduca*, and *cupulifex*. Generally a paler colour than *raphiduca* and *smeatoni* and possibly less hirsute. Specimens with everted foveae have been collected.

Male.—With palp as shown in Figure 11*B* (reproduced from Hogg (1903) with permission of the publishers).

At present the species is distinguished ecologically: it usually occurs in clay and in situations which are subject to flooding and has a saucer-shaped soil door as shown in Plate 1, Figure 2. Specimens from certain localities, e.g. Laverton, W.A., have the door “dropped” below the rim of the burrow. Although the hinge is situated on the rim, the free edge of the door hangs at an angle of about 45° to the hinge line (see Plate 6, Figs. 1 and 2).

Types.—Holotype male from Roebourne, W.A., in the British Museum of Natural History (not seen). Allotype female (herein designated and described) from Zanthus, W.A., collected from burrow by A. R. Main, 5.x.1956 (B.M. 56/558), to be deposited in Western Australian Museum. Door of allotype also to be deposited in Western Australian Museum.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Coolawanyah (Fortescue R.), 1; Roy Hill, 1; north-west coastal highway, 23 miles N. of Murchison R., 2; Greenough R., Geraldton–Mullewa Rd., 2; Merkanooka, 4; Morawa, 2; Woolaga Creek (east of Mingenew), 1; Gullewa, 8 miles N. of, 1; Mt. Magnet, 30 miles E. of, 8; Paynesville, 14 miles S. of, 1; Great Northern Highway, Paynes Find, 24 miles SW. of, 1; Lake King Dowak track, 27 miles E. of 90 Mile Tank, 1; Peak Charles, 24; Kumarl, 4 miles W. of, 1; Kurrawang, 1; Emu Rock, 35 miles S. of Coolgardie, 1; Young R., Ravensthorpe Esperance Rd., 1; Ravensthorpe, 7 miles S. of, 1; Borden, several miles N. of, 1; Stirling Range, S. base of Bluff Knoll, 8; Norseman, 6 miles N. of, 1; Norseman, 55 miles E. of (Eyre Highway), 1; Fraser Range (66 mile peg, Eyre Highway), 1; Fraser Range (73 mile peg, Eyre Highway), 1; Fraser Range (78 mile peg, Eyre Highway), 1; Comet Vale, a few miles N. of, 2; Laverton, 2 miles W. of, 11; Randells, 10 miles W. of, 1; Randells, 9 miles W. of, 1; Karonie, 1; Coonua, 15 miles E. of, 3; Zanthus, 12 miles W. of, 2; Zanthus, 2 (includes allotype); Cundeelee Mission, 2 miles NE. of, 1; Balladonia, 20 miles W. of, 1; Balladonia, 9 miles E. of, 1; Balladonia, several miles S. of, 2; Mt. Ragged, 10 miles SE. of, 3; Caiguna Tank, 24 miles W. of, 1; Cocklebiddy Tank, 1; Madura, 13 miles E. of, 1; Eucla, 22 miles W. of, 2; Eucla, a few miles W. of, 1. SOUTH AUSTRALIA: Bunabie Tank, 6 miles E. of, 1; Albula Karoo Tank, 1; Yangoonabie Tank, 2 miles E. of, 1; Yangoonabie Tank, 3 miles E. of, 1; Mallabie Tank, 3 miles E. of, 8; Ivy Tanks, 14 miles E. of, 2.

A. occidentalis (?)

Females or immature specimens.—WESTERN AUSTRALIA: Moonera Tank, 13 miles W. of, 1; Madura, 13 miles E. of, 1. SOUTH AUSTRALIA: Iron Knob, 11 miles W. of (road through Gawler Range), 1.

Remarks.—*A. occidentalis*, described from a male specimen, is the only species of *Aganippe* mentioned in the literature from the north-west of Western Australia. Hogg knew nothing of its biology but subsequently only one biological form has been

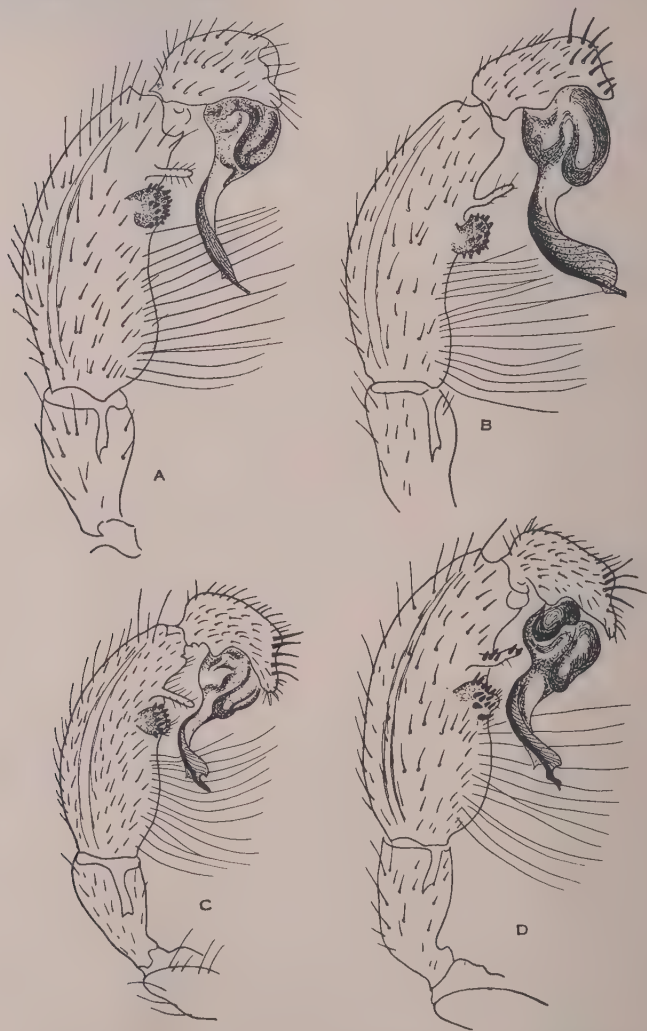


Fig. 12.—Retrolateral aspects of right pedipalps of male specimens of aganippines: *A*, *Aganippe cupulifex*, sp. nov. (holotype). *B*, *Ag. raphiduca* Rainbow & Palleine, type race (topotype, B.M. 53/318); *C*, *Ag. raphiduca*, intermediate between type and proto-*Idiosoma* races (B.M. 54/31); *D*, *Idiosoma nigrum* Main (allotype).

collected from this area, thus it is deduced to be conspecific with *occidentalis*. *A. simpsoni* is tentatively synonymized with *occidentalis* because it appears from field work that only the claypan-adapted form (i.e. *occidentalis*) is likely to occur in the region from which Hickman's species was collected.

AGANIPPE RAPHIDUCA Rainbow & Pulleine

Aganippe raphiduca Rainbow and Pulleine, 1918, Rec. Aust. Mus. 12; 93-5, pl. 21, figs. 38-42.

Aganippe latior Rainbow and Pulleine, 1918, op. cit. 12: 90, 92 (incorrectly identified).

Diagnosis.—*Female*: Generally, morphologically indistinguishable from females of *smeatoni*, *occidentalis*, and *cupulifex*.

Male.—The palpal stigma of the "type" race has a wide flange and when viewed retrolaterally a small pointed subterminal spur is visible on the lower side (see Figs. 7D and 12B). The stigma of the two races designated below as "twig-lining" and "proto-*Idiosoma*" is like that of *Idiosoma* (see below).

TABLE 7
PRINCIPAL CHARACTERISTICS OF THE FOUR RACES OF AGANIPPE RAPHIDUCA

Character	Type Race	Proto- <i>Idiosoma</i> Race	Twig-lining Race	Rottnest Race
Abdominal sigilla (pairs)	2	4	2	2
Abdominal spines	None	Present	None	None
Eyes	See Figure 25	See Figure 25	See Figure 25	See Figure 25
Male palp	See Figures 7D, 12B (like holotype)	See Figure 12D (like <i>Idiosoma</i>)	See Figures 12D, 13D (tending to be like <i>Idiosoma</i>)	Like type race
Habitat	Riparian or clay flats (moist situation)	Linear litter (dry situation)	Spatulate or linear litter (dry situation)	Usually swamp environment (moist situation)
Door	Soil, flap or cork-like (Plate 1, Fig. 3)	Twig, wafer-like	Twig, inset or wafer-like (Plate 4, Figs. 1 and 2)	Soil, inset
Burrow entrance inclination	Inclined	Vertical	Slightly inclined to vertical	Inclined
Rim of burrow	Without twigs	With twigs	With twigs*	Without twigs

* See also Figure 23E for typical shape of lower burrow.

Morphological variation.—This species is polytypic, containing at least four contiguous races. For convenience these are referred to as "type", "Rottnest", "proto-*Idiosoma*", and "twig-lining" races respectively. The morphological and biological characteristics of the races are presented in Table 7. The distribution of these races in relation to available habitats is presented diagrammatically in Figure 20.

Types.—Male and female types from King's Park, Perth, collected by R. Pulleine, 21.v.1912, in the Australian Museum. No. K40845 for both types (both seen by the author). A female specimen labelled "co-type", also in the Australian Museum (No. K40846), locality, collector, and date as above.

*Specimens examined**Type Race*

Females and immature specimens.—WESTERN AUSTRALIA: Albany Highway, 164 mile peg, 1; Donnelly's Camp, 1; Donnelly's Camp, 9 miles E. of, 3; Northcliffe, 1; Kirup, 2; Boyanup, 2; Bridgetown, 7 miles W. of, 1; Balingup, E. of, 6; Balingup, S. of, 5; Balingup, W. of, 6; Donnybrook, 2; Asplin, 2; Eulin, 1; Qualeup, 1; Warrening Gully, 1; Quindanning, 2 miles W. of, 2; Tallanalla, 14 miles NE. of (Harvey-Quindanning Rd.), 1; Brunswick Junction, 62; Hotham R., about 8 miles SE. of Marradong, 1; Coolup, 1; Pinjarra, E. of, 5; Pinjarra, S. of, 2; Dwellingup, 4; Crossman, 1; Dwarda, 2; Brookton, 4 miles S. of, 1; Karragullen, 18 miles SE. of (Brookton-Kelmscott Rd.), 2; Jarrahdale, 22; Byford, 1; Canning Valley (Roleystone), 6; Araluon, 1; Churchman's Brook, 8; Bibra Lake, 2; Kowdale, 1; Inglewood, 1; Armadale, 1; Walyunga Pool, 2; Bullsbrook (scarp front), 3; Muchea, 6; Giddegannup, 2; York, 5 miles E. of, 2; Kauring, 1; Quairading, 13 miles E. of, 1; Lomos, 1; Corrigin, 15 miles W. of, 1; Goomalling, 2; Wyalkatchem, 12 miles W. of, 1; Dandaragan, 2; Dandaragan, about 20 miles NW. of (track to Jurien Bay), 1; Koodiewoodie Range, 1; Great Northern Highway, 57 mile peg, 1; Moore R., 10 miles E. of Mogumber, 1; New Norcia, 9 miles E. of, 3; Calingiri, 3 miles N. of, 1; Walebing, S. of, 3; Walebing, 5 miles E. of, 8; Walebing, 7 miles E. of, 1; Walebing, 1 mile N. of, 1; Walebing, 2 miles N. of, 1; Walebing, 3 miles N. of, 2; Walebing, 5 miles N. of, 2; Watheroo, 4 miles E. of, 1; Coorow, 1; Three Springs, 1; Bindi Bindi, 7; Geraldton Highway, 158 mile peg, 1; Wongan Hills, 3; Nittymarra Hill, W. of, 1.

Males.—WESTERN AUSTRALIA: Jarrahdale, 1; King's Park, Perth, 1; Brunswick Junction, 7; Bickley, 1.

Rottnest Race

Females and immature specimens.—WESTERN AUSTRALIA: Rottnest I., 38.

Males.—WESTERN AUSTRALIA: Rottnest I., 1.

Proto-Idiosoma Race

Females and immature specimens. WESTERN AUSTRALIA: Dwarda, 2; Brookton, 24 miles NW. of (Brookton-Kelmscott Rd.), 1; Karragullen, 24 miles SE. of (Brookton-Kelmscott Rd.), 1; Karragullen, 10 miles SE. of (Brookton-Kelmscott Rd.), 1; Red Hill Rd., edge of scarp, 1; Upper Swan, 1; Mt. Helena, 1; Darlington, 1; Coorow, 1; Three Springs, 3; Beatty, 3; Camu, 1; Kadi Gate, 2; Gullewa, 4 miles N. of, 1; Great Northern Highway, rabbit-proof fence E. of Wubin, 2; Great Northern Highway, 13 miles SW. of Paynes Find, 1; Paynes Find, 2 miles E. of, 1; Great Northern Highway, 6 miles NE. of Paynes Find, 1; Great Northern Highway, 28 miles NE. of Paynes Find, 1.

Males.—WESTERN AUSTRALIA: Paynes Find, 2 miles E. of, 1.

Type Race-Proto-Idiosoma Race Intermediates

Females and immature specimens.—WESTERN AUSTRALIA: Borden, 2; Borden, 1 mile S. of, 1; Borden, 5 miles S. of, 2; Borden, 13 miles S. of, 4; Mongup Spring (Stirling Range), 12 miles N. of, 1; Chirelillup Creek, N. of Formby, 4; Katanning, 6 miles N. of, 4; Dryandra, 1; Williams, 13 miles S. of (Albany Highway), 7; Williams, 1; Brookton, 6 miles S. of, 4; Popauyinning, 4 miles S. of, 7; Brookton, 24 miles NW. of (Brookton-Kelmscott Rd.), 4; Merredin, several miles E. of, 1; Merredin, 5 miles N. of, 2; Merredin, 5.5 miles N. of, 1; Merredin, 8 miles N. of, 1; Bruce Rock, 13 miles N. of, 2; Noongar, 6; Jilakin Rock, 4 miles N. of, 2; Jilakin Rock, 1; The Humps (Hyden), 1; Wyalkatchem, 17 miles SE. of, 1; Wyalkatchem, 1 mile S. of, 1.

Males.—WESTERN AUSTRALIA: Katanning, 6 miles N. of, 1; Jilakin Rock, 1; Dryandra, 1.

Twig-lining Race

Females and immature specimens.—WESTERN AUSTRALIA: Paynes Find, 2 miles E. of, 2; Sandstone, 9 miles W. of, 6; Lawlers, 6 miles W. of, 1; Leonora, 17 miles NW. of, 11; Cardinia Creek, 6; Malcohn, 10 miles E. of, 4; Laverton, 8 miles W. of, 1; Laverton, 2 miles W. of, 1;

Bulong, 4 miles S. of, 3; Bulong, 5 miles SE. of, 2; Bulong, 10 miles W. of, 1; Higginsville, 6 miles S. of, 4; Norseman, 1; Salmon Gums, 6 miles S. of, 7; Newdegate, 6 miles W. of, 1; No. 1 rabbit-proof fence, $\frac{1}{2}$ mile E. of gate on Lake King-Dowak track, 1; Lake King-Dowak track, 20 miles E. of 90 Mile Tank, 1; Lake King-Dowak track, 23 miles E. of 90 Mile Tank, 2; Peak Charles (east) track, 2 miles S. of turnoff from Lake King-Dowak track, 1; Peak Charles, 1; Golden Ridge, 11 miles E. of, 1; Coonana, 6 miles E. of, 1; Zanthus, 1; Queen Victoria Spring, 5 miles SW. of, 1; Cundelee Mission, 3 miles NE. of, 1; Norseman, 8 miles E. of, 1; Fraser Range, 78 mile peg, Eyre Highway, 1; Magooinya (Balladonia), 1; Boonanya, 12 miles S. of, 1; Pine Hill, (Nanambinia-Israelite Bay track), 1; Israelite Bay, 11 miles NW. of, 3.

Males.—WESTERN AUSTRALIA: Bulong, 5 miles SE. of, 1; Cardinia Creek, 1; Laverton, 2 miles W. of, 1.



Fig. 13.—Right pedipalps, retrolateral aspect, of male *Aganippe* specimens: A, *Ag. raphiduca* Rainbow & Pulleine (?), aberrant specimen (B.M. 56/174); B, tip of stigma of same, enlarged; C, *Ag. cupulifex*, sp. nov., stigma of twig-lining specimen (B.M. 56/272); D, *Ag. raphiduca*, twig-lining race, stigma (B.M. 56/74).

A. raphiduca (?)

Aberrant male specimen.—WESTERN AUSTRALIA: Albany Highway, 164 mile peg, 1.

A. raphiduca (?) (*type race* ??)

Females and immature specimens.—WESTERN AUSTRALIA: Diminup, 1; 13 miles E. of Albany Highway, on road to Wagin, 3; Emu Hill (Narembeen), 1.

Males.—WESTERN AUSTRALIA: Goomalling, 1.

Remarks.—*Aberrant specimens:* (i) A single specimen with everted fovea has been collected. (ii) An aberrant male specimen was collected from the 164 mile peg, Albany Highway. This specimen was under casuarinas, where a normal female specimen of *A. raphiduca*, with an inset soil door was collected. The door of the male was not observed. The male had a bifurcated tip on each palpal stigma (Fig. 13B). This abnormality probably indicates that the animal would not be able to make a successful mating. Also the processes on the palpal tibia were completely atypical for *Aganippe*. Instead of the usual upper digital apophysis and the lower, spined, burr-like process there was a single, median, spined process, with a group of distal spines on the tibia above it (Fig. 13A). Thus the whole tibia was much like that of

E. latior. The specimen may be an intergeneric hybrid between *A. raphiduca* and *E. latior* (*latior* specimens were collected a few chains away at the same general site).

AGANIPPE CUPULIFEX, sp. nov.

Diagnosis.—*Female*: This is a biological species with little morphological distinction from the type race of *raphiduca* or the females of *occidentalis* and *smeatoni*. It is often a paler colour and less hirsute than *raphiduca*, by which character it resembles *occidentalis*.

Male.—The male when allopatric to *raphiduca* has the palpal stigma exactly the same as that of *raphiduca*. When the two are sympatric the stigma of *cupulifex* is different, having only a very narrow flange on one side, with a larger, more conspicuous spur opposite near the tip (Figs. 7F and 12A). The only twig-lining male specimen collected (from 15 miles S. of Coolgardie, which area overlaps the range of the twig-lining race of *raphiduca*) has a stigma similar to that of the type race of *raphiduca* but with the flange slightly narrower (Fig. 13C). Also on the tibia of the first leg in place of the characteristic apophysis there are a few heavy spines (Fig. 9B).

Species distinguished by dome-shaped soil door. This may be a high dome (Plate 2), either inset into the rim of the burrow or overlapping a flanged rim, or it may be a depressed dome as when the specimens are twig-lining in which case it overlaps the rim (Plate 3, Figs. 1 and 2).

Types.—Holotype male and allotype female (herein designated and described) collected by the author from burrows at 45 mile peg, Great Northern Highway, W.A. Holotype collected 3.iv.1953 (B.M. 53 29), allotype collected S.v.1955 (B.M. 55 284). Both types and door from burrow of holotype to be deposited in the Western Australian Museum.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Great Northern Highway, 45 mile peg, 22 (includes allotype); Chittering Lakes, Great Northern Highway, 4; Cullalla, 1; Avon Valley, near Jumping Hill, 11; Toodyay, 6 miles W. of Rod Hill Rd., 2; Wongamine, 18; Mt. Dick, 3; Mt. Dick, several miles NE. of, 1; Bolgart, 9.5 miles SW. of, 1; Bolgart, 8 miles SW. of, 1; Bolgart, 7 miles W. of, 1; Calcarra, 1; Walebing, 5 miles E. of, 3; Wubin, 2 miles E. of, 3; West Yorkrakine, 1; Bungulla, 9 miles N. of, 18; Enni Hill, near Narembeen, 1; Bordering, 4 miles W. of, 6; Bruce Rock, 1; Bruce Rock, 8 miles N. of, 2; Merredin, 5; Merredin, 6 miles N. of, 1; Elabba, 1; The Humps, Hyden, 5; Hyden, 6 miles NE. of, 2; Karlgarin, 11 miles W. of, 3; Newdegate, 17 miles E. of, 1; Newdegate, 23 miles E. of, 1; Newdegate, 26 miles E. of, 1; 35 miles E. of 90 Mile Tank on Lake King Dowak track, 1; Noongar, 2 miles W. of, 1; Bullabulling, 3; Boerabbin, 3; Coolgardie, 18 miles S. of, 3; Pioneer, 5 miles S. of, 2; Belong, 10 miles W. of, 2; Lakewood, 6 miles E. of, 2; Lakewood, 17 miles E. of, 1; Stoneville, about 4 miles E. of, 2; Randells, 9 miles W. of, 1; Randells, 15 miles E. of, 1; Norseman, 8 miles E. of, 1; Eyre Highway, 29 mile peg E. of Norseman, 1; Newman Rock, 1; Fraser Range Sta., west boundary gate on Eyre Highway, 1; Boomaya Rock, 4 miles S. of, 1; Junanda Rock, 1; Pine Hill, (Narabaminia-Israelite Bay track), 1; Junana Rock, 5 miles S. of (coastal plain), 1.

Males.—WESTERN AUSTRALIA: Great Northern Highway, 45 mile peg, 4 (includes holotype); Wongamine, 1; Bruce Rock, 2 miles N. of, 1; Merredin, 5 miles N. of, 1; Coolgardie, 15 miles S. of, 1.

A. cupulifex (?)

Female and juvenile.—WARRING, WESTERN AUSTRALIA: Brookman, 4 miles S. of 1; Walebing, 5 miles W. of, on N. side of Aron Valley, 1 (juv.).

INCERTAE SEDIS

Genus AGANIPPE Cambridge

"Walebing" Race

This name is applied for convenience to a population restricted so far as is known to a small area of geographic overlap of *cupulifex* and *capitadoca* around Walebing and Bindi Bindi, W. A. Characterized by soft dors of indistinct outline and slightly inset into furrow.

Females morphologically indistinguishable from *capitadoca* and *cupulifex* but the male quite distinct. Stigma of palp very like that of *cupulifex* (when compared with *capitadoca*) but that of base of leg looks equal aggregation characteristic of the genus, having in its place several heavy spines (Fig. 10). At present this form thought to be a hybrid between *capitadoca* and *cupulifex*.

Specimens examined

Females and juveniles.—WARRING, WESTERN AUSTRALIA: Walebing, 1 mile S. of 1; Walebing, 5 miles E. of, 4; Bindi Bindi, 3.

Males.—WESTERN AUSTRALIA: Walebing, 5 miles E. of, 2.

Other Hybrids (?)

Four other specimens are also thought to be hybrids between *A. capitadoca* and *cupulifex*.

Specimens examined

Females.—WARRING, WESTERN AUSTRALIA: Great Northern Highway, 30 miles S. of 1, Brookton-Kalamott Rd., near Waranine Brook, 3.

Aganippe Population from Southern Corner of Eyre Peninsula, S. A.

Female specimens of *Aganippe* collected from this region are tentatively included in *euleriana* although they differ morphologically, particularly regarding the enlarged eyes found the Flinders Range and Mr. Luby Range specimens.

Specimens from End of the Flinders Range

Rancho and Pullen (1935) described two species of *Aganippe* (female) and several from Ethereld, Qld. (already discussed). The Queensland Museum has a female specimen of *Aganippe* (adult) from near Ethereld, Qld. However due to its morphological similarity to certain of the western species and absence of biological data a name cannot with certainty be attributed to this specimen.

The National Museum possesses several specimens of the genus *Aganippe* from New South Wales and the Mallee region of Victoria. These are probably *euleriana*. The author has collected numerous male and female specimens from western South Australia and western Victoria. These are at present considered to belong to

sulzeistis and *smeatoni*. Much field information is necessary before the eastern complex of the genus can be discussed fully.

Genus IDIOSOMA Ausserer

- Idiosoma* Cambridge, 1870 and partem *sigillatum*, Proc. Zool. Soc. Lond. 1870: 105-7, pl. 8, fig. 2. Rainbow, 1901, Rec. Aust. Mus. 4: 7.
Idiosoma Ausserer, 1871, Verh. zool.-bot. Ges. Wien 21: 150. Koch, 1871, Die Arachniden Australiens 1: 461-3. Pocock, 1897, Ann. Mag. Nat. Hist. (6) 19: 109-12. Hogg, 1901, Proc. Zool. Soc. Lond. 1901 (2): 230; 1902, op. cit. 1902 (2): 125, pl. 13, fig. 8. Simon, 1903, Hist. Nat. Araig., Suppl. Gen., p. 901-2, fig. 1053. Rainbow, 1912, Rec. Aust. Mus. 9: 110-11. Main, 1952, W. Aust. Nat. 3: 130-7, pl. 1, text-figs. 1, 2. *Acanthosoma* Simon, 1892 and partem *sigillatum* Hist. Nat. Araig. 1: 91. Rainbow, 1901, Rec. Aust. Mus. 4: 7.

Type species *Idiosoma sigillatus* Cambridge, 1870.

Diagnosis.—Differs from *Eucryptops* and *Avidiops* by presence of dorsal abdominal sigilla. Differs from *Aganippe* by having abdominal corrugations; also by having 4 pairs of sigilla (anterior 2 pairs may be degenerate), whereas *Aganippe* only rarely has the posterior 2 pairs developed.

Male specimens have always several spines on the upper digital apophysis of the palpal tibia. These spines were omitted from the figure of an *I. sigillatum* palp (specimen W.A. Museum catalogue No. 39-2154) (Main, 1952, text-fig. 1a). Re-examination of this specimen showed spines to be present. Such spines are only rarely present in *Aganippe*.

Idiosoma is an obligatory twig-liner. The burrow profile is always of characteristic shape as illustrated in Figure 23A.

IDIOSOMA SIGILLATUM (Cambridge)

- Idiosoma sigillatus* Cambridge, 1870, Proc. Zool. Soc. Lond. 1870: 105-7, pl. 8, fig. 2. Rainbow, 1901, Rec. Aust. Mus. 4: 7.
Idiosoma sigillatum Ausserer, 1871, Verh. zool.-bot. Ges. Wien 21: 150. Koch, 1871, Die Arachniden Australiens 1: 461-3. Pocock, 1897, Ann. Mag. Nat. Hist. 6 19: 109-12. Hogg, 1901, Proc. Zool. Soc. Lond. 1901 (2): 230; 1902, op. cit. 1902 (2): 125, pl. 13, fig. 8. Simon, 1903, Hist. Nat. Araig., Suppl. Gen., pp. 901-2, fig. 1053. Rainbow, 1912, Rec. Aust. Mus. 9: 110-11. Main, 1952, W. Aust. Nat. 3: 130-2, 135-7, figs. 1a, b, c; 2a.
Acanthosoma sigillatum Simon, 1892, Hist. Nat. Araig. 1: 91. Rainbow, 1901, Rec. Aust. Mus. 4: 7.

Diagnosis.—*Female*: Differs from *I. nigrum* by a lesser degree of abdominal sclerotization, by having brown ridges and yellowish grooves, and by nature of spines (see Fig. 14C).

Male.—Morphological differentiation from *I. nigrum* doubtful, palpal and first tibial structures appear essentially the same as shown in Figure 12D. *I. sigillatum* appears to be very slightly larger. Range in carapace length 8.40-10.50 mm. Since the forms are allopatric there is no possibility of hybridization in the field.

Types.—Holotype male from the Swan R., W.A., received by the British Museum of Natural History through S. Stevens in 1864 (not seen). Pocock (1897, p. 112) restricts the above locality to Perth. Allotype female (described by Pocock

(1897)) from Perth, collected by H. W. J. Turner, in the British Museum of Natural History (not seen).

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Inglewood, 1; King's Park, 1; Rockingham, E. of railway crossing, 2; Rottnest I., 1; Muchea, 7 miles N. of, 1; Muchea, 5 miles N. of, 1; Chatterbox Lakes, 1; Gillingarra, 1; Mogumber, 1; Mogumber, 5 miles E. of, 1; Koolberridge Ranges, 1; Mt. Murray, W. of Moora, 1; Gillingarra, 1; Bolgart, 9.5 miles SE. of, 1.

Males.—WESTERN AUSTRALIA: Fideat Park, 1; West Midland, 1; Naval Base, 1; Mt. Hawthorn, 1.

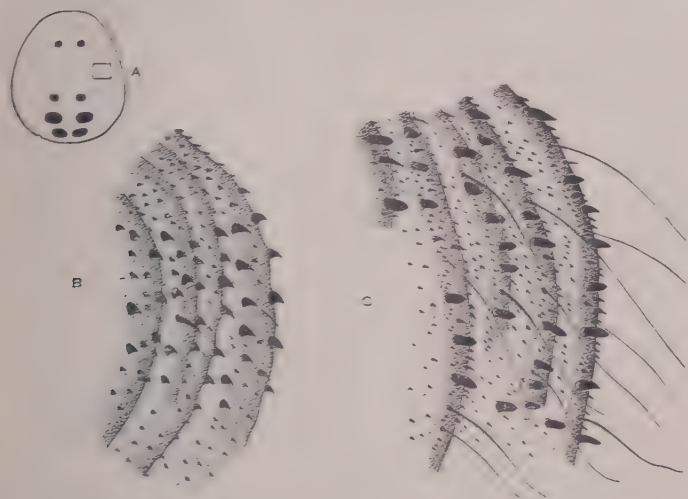


Fig. 14.—Abdominal spination of *Idiosoma*, female specimens. A, approximate region of abdomen from which drawings were made; B, *I. nigrum* Main; C, *I. sigillatum* Cambridge.

IDIOSOMA NIGRUM Main

Idiosoma nigrum Main, 1952, W. Aust. Nat. 3: 133, 135–6, pl. 1, text-fig. 2c.

Diagnosis.—*Female*: Differs from *sigillatum* by having a greater degree of abdominal sclerotization and uniform black colour (in life). Dorsal spination of abdomen as shown in Figure 14B.

Male.—Morphological differentiation from *sigillatum* doubtful. It is usually a little smaller but not enough specimens have been collected to definitely separate the two species on size alone. Range in carapace length 6.90–9.00 mm.

Types.—Holotype and paratype designated and described by Main (1952) collected by the author on 19.vi.1952 from the Wongan Hills, W.A. Holotype (B.M. 52 132) deposited in the Western Australian Museum; paratype (B.M. 52 147) deposited in the Australian Museum. Allotype male (herein designated and described) collected by G. F. Best, from Koorda, W.A., deposited in the Western Australian Museum, No. 40-1070.

Specimens examined

Females and immature specimens.—WESTERN AUSTRALIA: Connolly Gully (Brookton-Kelmscott Rd.), 1; Flint Gully, S. of (Brookton-Kelmscott Rd.), 1; Avon Valley, near Jimperding Hill, 4; Northam, 1; Toodyay, 6 miles W. of (Redhill Rd.), 3; Mt. Dick, 3; Goomalling, 1; York, 18 miles E. of, 1; Quairading, 1; Bungulla, 9 miles N. of, 4; Wyalkatchem, 17 miles SE. of, 1; Wyalkatchem, 1 mile S. of, 2; Minnivale, 1; Bolgart, 1; Bolgart, 7 miles W. of, 2; Botherling, 1; Calcarra, 1; Nittymarra Hill, W. of, 1; the Wongan Hills, 10; Walebing, 5 miles E. of, 1; Walebing, 7 miles E. of, 3; Bindi Bindi, 3; Watheroo, 4 miles E. of, 3; Woolaga Creek, east of Mingenew, 2; Dalwallinu, 6 miles N. of, 1; Gutha, 17 miles NE. of, 2; Canna, 2; Gullewa, 8 miles N. of, 1; Ederga, 4 miles E. of, 4; Mullewa, 12 miles W. of, 1; Mullewa, 18 miles S. of (Mingenew Rd.), 2; Galena, 2 miles N. of, 1; Galena, 2; Great Northern Highway, 17 miles NE. of No. 2 rabbit-proof fence, 2; Great Northern Highway, 5 miles N. of Mt. Gibson turnoff, 1; Paynes Find, 2 miles E. of, 8; Great Northern Highway, Paynes Find, 24 miles SE. of, 1.

Males.—WESTERN AUSTRALIA: Beverley, 1; Moora, 12 miles S. of, 4; Moora, 9 miles S. of, 1; Moora, 5.5 miles S. of, 1.

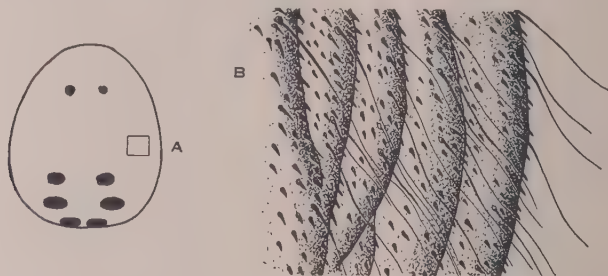


Fig. 15.—“*Idiosoma hirsutum*” Main (*I. sigillatum* × *Ag. raphiduca* (?)): A, approximate region of abdomen from which drawing was made; B, abdominal spination.

Remarks.—No apparent difference in structure of external reproductive parts of male specimens of the two *Idiosoma* species. Both as shown in Figure 12D. Although the abdominal cuticle is so distinct in females and juveniles of the two species, the dorsum of the abdomen in the males is very similar, the corrugations and sclerotization being reduced. Spination similar, long black scattered spines and a uniform covering of coarse but inconspicuous hairs.

INCERTAE SEDIS

IDIOSOMA HIRSUTUM Main

Idiosoma hirsutum Main, 1952, W. Aust. Nat. 3: 132–3, 135–7, text-fig. 2b.

The above is now considered to be a hybrid of *I. sigillatum* and the proto-*Idiosoma* race of *A. raphiduca*. The sex and species of the parents are unknown. Abdominal spination unlike that of *I. sigillatum* or *nigrum* (Fig. 15B). Differs from *Aganippe* by the presence of pronounced abdominal corrugations. Alternatively may represent an extreme form, such as has not been recorded during field collecting, of the proto-*Idiosoma* race of *A. raphiduca*.

Types.—Holotype and paratype (females) (designated by Main 1952) are in the Western Australian Museum (Nos. 29-1060 and 1914-1069 respectively).

Type locality.—Victoria Park; locality of paratype, South Perth.

(d) Identification Key

The following key is based on morphological and behavioural attributes. Only those forms of which the specific status is definite are included.

KEY TO GENERA AND SPECIES OF THE TRIBE AGANIPPINI

Females

1. With dorsal abdominal sigilla. Never with a sock (see Figs. 23B–23D) in the burrow. May or may not be twig-lining 5
Without dorsal abdominal sigilla. May or may not have a sock in the burrow. May or may not be twig-lining 2
- 2(1). Shape of carapace and abdomen roughly as in Figures 2A, 2B, and 3A. Without sock in the burrow. Never twig-lining Genus *Eucyrtops* ...3
Shape of carapace and abdomen roughly as in Figures 2C, 2D and 3B, 3C. With a sock in the burrow. May or may not be twig-lining Genus *Anidiops* ...4
- 3(2). With numerous heavy spines on the venter of palp and legs I and II (Figs. 4D–4F). Usually in a riparian habitat. Soil door flap-like (Plate 1, Fig. 1)*E. riparia*
Spines of palp and legs I and II not as above (Figs. 4A–4C). Black colour (in life). Matures at 5.50 mm. Never occurs in a riparian habitat. Fragile soil and litter door ..*E. latior*
Spines on palp and legs I and II not like *riparia*. Pale brownish colour (in life). Matures at 3.70 mm. Occurs under litter in mulga (*Acacia aneura*) country along braided creeks. Does not overlap range of *latior*. Soil door cork-like*E. eremaea*
- 4(2). With heavy spinules on at least maxillae, labium, and anterior part of sternum; may extend on to posterior part of sternum and coxae (Figs. 10A and 10C) ..*An. manstridgei*
If spinules present, on maxillae only*An. villosus*
- 5(1). No abdominal corrugations, with usually only 2 pairs of abdominal sigilla. May or may not be twig-lining Genus *Aganippe* ...6
Abdomen with corrugations, 4 pairs of sigilla (2 anterior pairs may be inconspicuous). Always twig-lining Genus *Idiosoma* ...9
- 6(5). Numerous cephalic bristles, eyes small and widespread as in Figure 25. Not known ever to be twig-lining*Ag. subtristis*
Few cephalic bristles, eyes not as above. May or may not be twig-lining 7
- 7(6). Never twig-lining. Soil door. Not known to occur west of the Flinders Range ..*Ag. smeatoni*
May or may not be twig-lining, door usually of soil, may be of litter material. Occur almost exclusively west of the Flinders Range 8
- 8(7). Dome-shaped soil door. Geographic range (so far as known) restricted to west of the Nullarbor Plain*Ag. cupulifex*
Soil door inset into rim of burrow, saucer-shaped with roundly bevelled margin (Plate 1, Fig. 2). May be "dropped" (Plate 6, Figs. 1 and 2)*Ag. occidentalis*
Door usually made of soil in which case flap-like or inset into rim of burrow (not saucer-shaped) (Plate 1, Fig. 3.) May have door made of twigs (Plate 4, Figs. 1 and 2). (Race differences of this polytypic species tabulated in Table 7)*Ag. raphiduca*
- 9(5). Ridges of corrugations usually brownish and grooves yellowish (ridges at least always dark, grooves pale). Small spines scattered over dorsum, large spines along ridges (Fig. 14C)*I. sigillatum*
Abdomen uniformly black. Spination as in Figure 14B. Heavy sclerotization sometimes partly obscures spination*I. nigrum*

Males

1. With dorsal abdominal sigilla 5
Without dorsal abdominal sigilla 2
- 2 (1). Palpal tibia with an upper digital apophysis and lower spined, burr-like apophysis. Stigma long, almost straight and pointed (Fig. 5A)*An. manstridgei*
If processes are present on palpal tibia they are not as above. Stigma short 3
- 3 (2). Palpal tibia with processes 4
Palpal tibia without processes (Figs. 5D and 8A) (except Stirling Range population)....
.....*E. riparia*
- 4 (3). Only one spined process on palpal tibia (Fig. 5C), stigma with slight terminal flange (Fig. 5E). Numerous spines on tibia distal to process. Range in carapace lengths 4.40-6.70 mm*E. latior*
Palpal tibia as above, stigma without terminal flange (Fig. 8C). Numerous spines on tibia distal to process. Range in carapace lengths 3.10-3.70 mm.....*E. eremaea*
Palpal tibia as above but with only about 6 spines distal to process (Fig. 8D, 8E) (Stirling Range population)*E. riparia*
- Two spined processes on palpal tibia (Fig. 5B)*An. villosus*
- 5 (1). With spines on upper digital apophysis of palpal tibia (Fig. 12D). Corrugated abdomen...
.....Genus *Idiosoma* ...9
Without spines on upper digital apophysis of palpal tibia (except proto-*Idiosoma* race of *Ag. raphiduca*). Abdomen without corrugations Genus *Aganippe* ...6
- 6 (5). Stigma strongly twisted like a corkscrew (Fig. 11A)*Ag. smeatonii*
Stigma not as above 7
- 7 (6). Stigma tapers to a point, dorsum of palpal tarsus covered with numerous short stout spines (Fig. 7C)*Ag. subtristis*
Stigma with flanges and palpal tarsus not covered with short stout spines 8
- 8 (7). Stigma with wide flange on the upper side and small spur opposite near tube-like tip (Figs. 12B and 7D) or as in Figures 12C or 13D (in which case spines may be present on upper digital apophysis of palpal tibia)*Ag. raphiduca*
Dome-shaped soil door. Stigma as in Figures 12B and 7D (when allopatric to type race of *raphiduca*). Stigma with narrow flange on upper side and relatively larger spur opposite near tip (Figs. 12A and 7F) (when sympatric with type race of *raphiduca*)*Ag. cupulifer**
Stigma as in Figure 11B (from Hogg 1903)*Ag. occidentalis*
- 9 (5). Range in carapace length 6.90-9.00 mm. See Figure 22 for geographic range*I. nigrum*
Range in carapace length 8.40-10.50 mm. See Figure 22 for geographic range; allopatric to *I. nigrum**I. sigillatum*

IV. NATURAL HISTORY

(a) Life History

The Aganippini are true "trapdoor" spiders. When the brood animals leave the parent burrow, they dig independent burrows and under normal circumstances live out their entire life history in the one burrow. As the animal grows it enlarges its burrow accordingly. Males and females build similar burrows. Females never leave their burrows; males vacate them only after maturity when they wander in order to mate, after which they die.

Mature aganippines exhibit marked sexual dimorphism. Apart from the copulatory structures on the palp, mature males also have longer, thinner legs and generally

* A youngling specimen had palp as in Figure 13C and no apophysis on 1st tibia as in Figure 9B.

a more spinose integument than do the females. Immature males and all females are structurally adapted to living in a tubular burrow (they have relatively short thick legs) but a mature male is adapted to running rapidly on the surface.

Moulting occurs in animals in the wild (juveniles, mature females, and males and females just reaching maturity) during early autumn. Mature males then wander with the first winter rains. However, a laboratory specimen of *An. villosus* collected in December 1952 has moulted annually during mid-summer on the following dates: December 18, 1953; December 24, 1954, and December 28, 1955. This animal was kept in a room at a constant temperature of 75°F. The humidity was not controlled.

Mating takes place during autum within the female's burrow. Only two groups of male animals have been collected while actually "wandering". These were six specimens of *I. nigrum* collected while "running" on May 25, 1954, between 10.30 p.m. and midnight during drizzling rain with an air temperature of 17.2°C. The other was a specimen of the type race of *Ag. raphiduca* collected on June 9, 1956, at 8.30 p.m. during drizzling rain with an air temperature of 12.0°C. All other specimens have been collected from the burrows before wandering, or amongst litter after wandering.

Males probably mate with several females since Baerg (1945, p. 106) observed tarantula males in the laboratory "mating as many as 12 times, and constructing 17 sperm webs".

Eggs are laid during late spring and early summer (October through November). The young emerge from the egg cocoon during mid-summer (late December through mid-January). The brood animals remain in the female's burrow until early winter, emerging only after substantial rains when the ground is wet and soft. Before egg laying, the female seals the door with silk. Some species, notably *An. villosus* and *E. riparia*, also plug the top of the burrow below the sealed door with a thick plaster of soil. Below this again *An. villosus* makes a complete new silk lining to the burrow which thus becomes a completely sealed cylinder. This seal is not broken until the following autumn, just before the young emerge. Neither the adult nor the young can therefore feed for several months. Young begin to feed immediately after constructing a burrow.

From field observations it is apparent that the reproductive behaviour of all species follows the same seasonal sequence. Females continue to breed in successive seasons. The egg cocoon is a flat disk and is attached vertically by strands of silk to the wall of the burrow in a swelling near the bottom in such a way as not to occlude the lumen, thus allowing the animal to pass up and down past it. Field data on reproductive capacity is available for 104 female specimens. Of these 19 had egg cocoons and 83 had broods (one specimen had a brood from the previous season still in the burrow with the next season's egg cocoon).

The range in number and diameter of eggs from individual cocoons and range in number and size of young from individual broods are presented in Table 8. More data are required before the size limits of eggs and brood young and the maximum number of eggs per cocoon of the various species can be characterized. It is possible that the species may exhibit geographic variation in this regard, or such features may depend on the age and size of the female parent.

(b) *Habitat Preferences and Ecological Distribution*

(i) *Habitat Characteristics and Preferences of Species.*—The numerous minor habitats occupied by aganippine species are grouped into four major categories as follows: spatulate litter, riparian, clay flats, and linear litter, the characteristics of which are discussed below.

TABLE 8
RANGES IN NUMBER OF EGGS IN INDIVIDUAL COCOONS, MEAN DIAMETER OF EGGS FROM INDIVIDUAL COCOONS, MEAN CARAPACE LENGTH OF YOUNG FROM INDIVIDUAL BROODS, AND NUMBER OF YOUNG IN INDIVIDUAL BROODS (WHEN TOTAL BROOD AVAILABLE)

Species	No. of Eggs	Mean Diameter of Eggs (mm)	No. of Cocoons	No. of Brood Young	Mean Carapace Lengths of Brood Young (mm)	No. of Broods
<i>Eucyrtops latior</i>	14-25	2.35-2.56	3	34-54	1.85-1.90	2
<i>E. crenata</i>	—	—	0	12-15	1.33-1.35	3
<i>E. riparia</i>	—	—	0	16 (?) - 80	1.32-1.65	18
<i>Eucyrtops</i> , "spinular" form	15	3.06	1	100-127	2.10-2.23	2
<i>Anidiops manstridgei</i>	14-66	2.88-3.10	4	—	—	0
<i>An. villosus</i>	—	—	0	42	3.06*	1
<i>Aganippe subtristis</i>	30	4.14	1	—	—	0
<i>Ag. smeatoni</i>	100	2.61	1	—	—	0
<i>Ag. occidentalis</i>	30-64	2.58-3.02	4	17-20	1.93-2.83	4
<i>Ag. raphiduca</i>						
Type race	—	—	0	55-126	1.70-1.93	23
Rottnest race	—	—	0	11-19(?)	1.75-1.83	2
Twig-lining race	23	1.87	1	28-31	2.36-2.42	2
Proto- <i>Idiosoma</i> race	—	—	0	17 (?)	3.10	1
Type proto- <i>Idiosoma</i> race	12	4.18	1	15-32	1.76†	1
<i>Ag. cupulifex</i>	39-75	2.43-2.46	3	68	1.60-1.88	10
<i>Idiosoma sigillatum</i>	—	—	0	66 (?)	2.73-3.05	3
<i>I. nigrum</i>	—	—	0	16 (?)	2.77-2.99	4

* Just hatched.

† Excluding one specimen, the brood young of which remained in the parent burrow for an unusually long period.

Spatulate litter.—Spatulate litter occurs in forest or woodland situations with a ground cover of eucalypt leaf litter. The litter is several inches deep, often matted together by fungus, and frequently having underlying humus, but the surface is loose and unbound. The litter is always of a permanent nature and is not disturbed by flood waters or wind. Such situations are relatively moist and harbour many cryptozoic arthropods, including beetles, which provide prey for the trapdoor spiders.

Riparian.—The small banks of creeks, roadside gutters, artificial drains, the vertical slopes at various levels of steep valleys, and the eroded terraces of river valleys all tend to provide moss-covered vertical faces ranging from a few inches

up to many feet in height. Such situations are usually composed of relatively soft or friable alluvial material and retain moisture throughout the dry summer. Many road banks and small streams support a greater density of spiders than the bigger creeks and rivers which have the steeper higher banks frequently aflood and crumbling with the fluctuating water levels. Due to the retention of moisture throughout the summer, the animals which form the diet of the spiders become aggregated into these situations, and hence the food supply is relatively uniform throughout the year.

Clay flats and claypans.—These general terms cover many minor habitats including the claypan depressions of the Nullarbor Plain, the wide, flat, barely perceptible valleys of the Darling Plateau, small clay flats around low hills, in fact any depression into which rain-wash and floods carry a deposit of alluvial material

TABLE 9
TYPES OF HABITAT IN WHICH AGANIPPINE SPECIES GENERALLY OCCUR

Species	Habitat Types			
	Spatulate Litter	Riparian	Claypans or Flood-flats	Linear Litter
<i>Eucyrtops lator</i>	+	—	—	+
<i>E. eremaea</i>	—	—	+	+
<i>E. riparia</i>	+	+	—	—
	(rarely)			
<i>Anidiops manatriges</i>	+	—	+	+
<i>Ac. villosus</i>	+	—	+	+
<i>Aganippe subtristis</i>	+	—	+	—
<i>Ag. australis</i>	—	+	+	—
<i>Ag. occidentalis</i>	—	—	+	+
<i>Ag. raphidiuca</i>	+	+	+	+
<i>Ag. cupulifex</i>	+	+	+	—
	(light litter)	(rarely)		
<i>Idiosoma sigillatum</i>	—	—	—	+
<i>I. nigrum</i>	—	—	—	+

* Mixed habitat of these two types favoured.

which consolidates into a clay texture. Such sites are subject to periodic sheet flooding; water may occasionally lie on the surface for several days. Scattered loose litter often occurs on the ground but always there occur in such places small patches of bare soil which is bound by a crust of algae and lichens. Some areas have large expanses with no litter at all.

Linear litter.—Linear litter occurs beneath such trees as *Callitriche* or *Acacia*, the "leaves" of which are long and thin. They usually occur in relatively dry situations and on poor soils. The main characteristic of such habitats is that they have a reduced food supply, so far as the spiders are concerned. It is in these habitats that twig-lining animals predominantly occur. *Callitriche* or *Acacia acuminata* or both

form isolated stands in forest or woodland associations. *A. aneura* trees (mulga) form a continuous environment in the dry interior. Usually the zone of stable litter which barely obscures the soil around the base of each tree is more or less discontinuous with that of the adjacent trees, forming again small "islands" in the general environment.

Table 9 shows the type of habitat in which the various species are generally found. Some species are adaptively plastic and occupy more than one type of habitat.

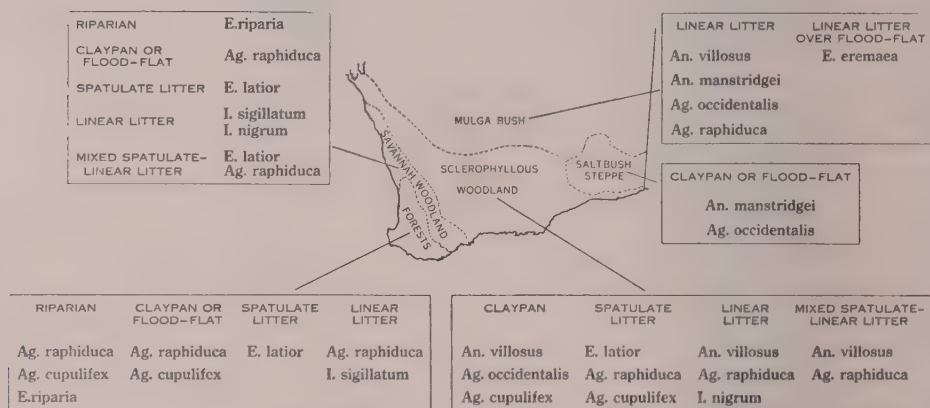


Fig. 16.—Habitat types available in zones of major vegetation formations of southern Western Australia and dominant species occupying these generalized habitats. Where more than one species is shown to occupy a given habitat type this does not necessarily imply sympatry (see also Figures 17–22 in which geographic ranges of individual species are given).

(ii) *Distribution in Relation to Availability of Habitats*.—The present discussion deals only with the Western Australian environment south of about the Murchison R., since it is this region which has been most extensively studied. Distribution of the aganippines is here dominated by a complex of ecological factors, geology, including topography and edaphic factors, rainfall, and vegetation. Of these the vegetation generally typifies the environment, therefore the ecological distribution of the spiders is here interpreted in relation to the major vegetation formations as delimited by Gardner (1944). A generalized picture of the ecological distribution of the Aganippini, i.e. in relation to the available habitat types within the zones of the major vegetation formations, is presented in Figure 16.

(c) Geographical Distribution of Species

The localities of all specimens in the author's collection from Western Australia in the region delimited for the ecological distribution are shown on the following figures: *Eucyrtops* (*latior*, *eremaea*, and *riparia*) (Fig. 17), *Anidiops* (*manstridgei* and *villosus*) (Fig. 18), *Aganippe occidentalis* (Fig. 19), *Ag. raphiduca* complex (Fig. 20),

Ag. cupulifex (Fig. 21), and *Idiosoma* (*sigillatum* and *nigrum*) (Fig. 22). The distribution of the twig-lining behaviour pattern in those species in which it is facultative is also indicated on the figures.

(d) *Construction and Maintenance of Burrows*

The initial construction of a burrow by a brood animal takes the following sequence of stages: excavation to the depth of the animal's body, door construction, indefinite deepening, and finally, after several months and perhaps not for about a

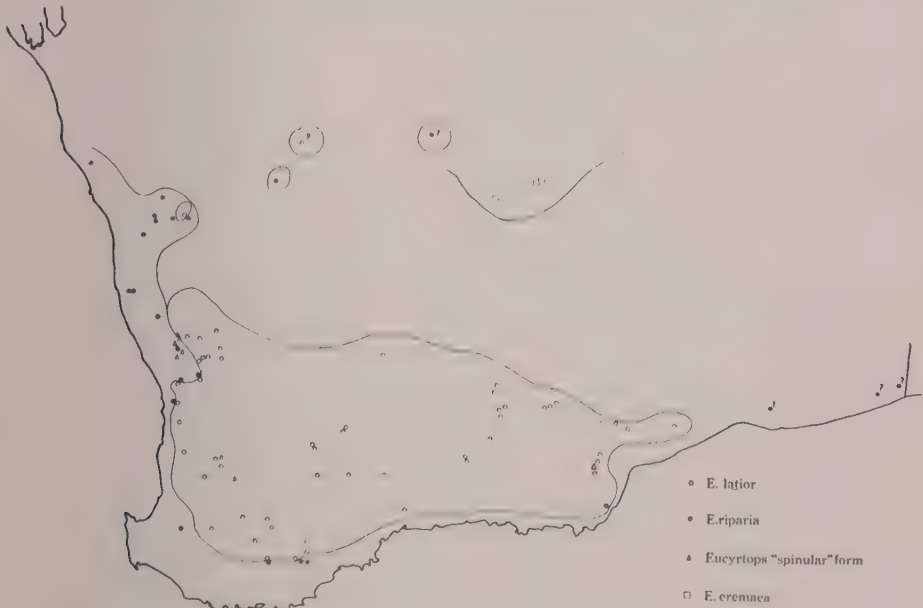


Fig. 17.—Geographical distribution of the species of *Eucyrtops* Pocock in Western Australia.

year, the application of a continuous, stout silk lining. When burrowing the spider breaks up the soil with its rastellum, then picks up the particles between the chelicerae and carries them to the edge of the burrow. The particles of soil are then pushed away by the palps and fore legs. Doors are built by constructing a ledge or veranda on one side of the burrow until the free edge meets the rim on the opposite side. This is made from particles of soil, or in some cases litter debris, which are bound with web.

Animals have been observed deepening their burrows and enlarging the rim and door by adding soil or twigs to the edge, but the actual enlargement of the burrow diameter has not been seen.

Damage to door and rim of the burrow is quickly repaired. Torn-off doors have sometimes been observed to be reattached with the original free margin of the door webbed down to the hinge of the burrow. Young animals disturbed from their

burrows will initiate another burrow but larger animals are incapable of beginning a new burrow although the capacity to repair a damaged burrow is retained throughout life. Twig-lining animals, when observed in the laboratory making their initial burrow, attach at least some twigs to the rim of the burrow before a door is constructed. However, other young animals taken from their burrows in the field construct a door before attaching twig lines when they dig secondarily in the laboratory. Attachment of twig lines is apparently part of the initial burrow-excavation process, but for animals with established burrows maintenance of a door (defence) is paramount over maintenance of intact twig lines (feeding). When attaching twig lines, animals at first seize, one by one, all twigs within reach of the burrow. By holding

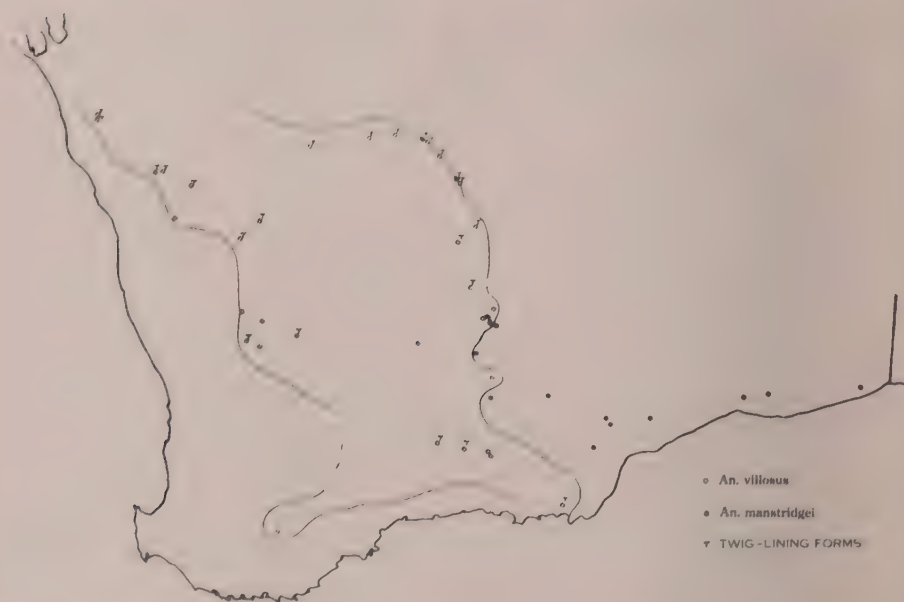


Fig. 18.—Geographical distribution of the species of *Anidiops* Pocock in Western Australia.

on to the rim of the burrow with the tarsal claws of the fourth legs they move the anterior part of the body about feeling for twigs with their palps and front legs. If insufficient twigs are available from this distance the animal actually leaves the burrow and searches over a distance of several inches for twigs which are then dragged back to the burrow, one end of the twig usually being held by the chelicerae and pedipalps. It is a comical sight to see a tiny spider with body length of less than half an inch dragging a comparatively "huge" pole three inches long back to its burrow and then hoisting one end of the twig on to the rim and holding it in position while binding it down with silk.

(e) Burrow Associates

Long-established burrows usually support a large number of terrestrial mites. These feed on the rejectamenta left in the burrows, breaking it down until only hard chitinous material remains. By actively disposing of the moist remnants of food debris these mites prevent the growth of fungi in the burrows. Occasionally spiders have attached to their bodies encrustations of mites, especially on the sternum and around the fovea.



Fig. 19.—Geographical distribution of *Aganippe occidentalis* Hogg in Western Australia.

(f) Habitat Selection

The general assumption is that animals, although observed to occupy “preferred” habitats, do not come to occupy such habitats as a result of choice but simply that young animals occupying habitats to which they are ill-adapted are selected against during their early life history. There is some evidence that trapdoor spiders do exert a choice in the type of habitat which they occupy, e.g. twig-lining forms of *Ag. raphiduca* and *An. villosus* in mulga country. In a uniform mulga environment the litter zone of a single tree or small clump of trees is completely isolated from the litter zone of adjacent trees. Here the spiders occupy the litter zones but never the bare intervening ground.

Either the dispersing young burrow in both bare and littered ground, those in the bare ground dying early from starvation, or the dispersing young burrow only when they come to littered ground.

Brood specimens of *I. nigrum* (exclusively twig-lining) returned to the laboratory and placed in a dish containing areas of littered and unlittered soil, i.e. given a choice of habitat, burrowed in littered soil. The inference from both field

and laboratory observations is that probably some of the spiders do actively select the habitat.

Trapdoor spiders, because of their close dependence on edaphic factors and type of leaf litter, are an ideal group with which to study the apparent selection of habitat. Further analysis of this aspect of behaviour is continuing with the *Aganippini*.

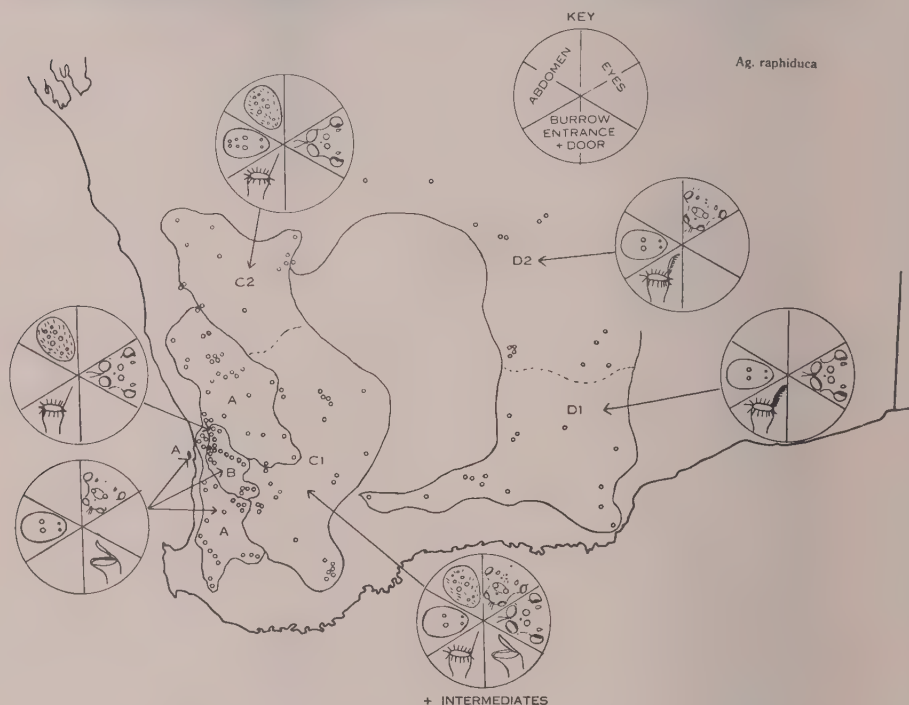


Fig. 20.—Geographical distribution of the adaptive races of *Aganippe raphiduca* Rainbow & Pullene in Western Australia showing the morphological and behavioural combinations occurring in the different regions. The types of habitat in the outlined regions are as follows: A, riparian and clay flat or swamp (i.e. moist); B, riparian and clay flat (moist) and linear litter (dry); C1, litter/clay flat (intermediate, moist/dry); C2, linear litter (dry); D1, spatulate litter (moderately dry); D2, linear litter (dry, semi-desert). The occupant races of these various regions are as follows: A, Rottnest (Rottnest I. only) and type (mainland only); B, type (moist habitats) and proto-*Idiosoma* (dry habitats); C1, intermediates between type and proto-*Idiosoma*; C2, proto-*Idiosoma*; D1, D2, twig-lining race.

(g) Defence Behaviour

The usual defence reaction of any aganippine is to hold the door firmly closed. This is achieved by placing the anterior end of the body in proximity to the door with the ventral surface facing the hinge and then pulling on the door with the tarsal claws of the palps and first two pairs of legs and perhaps additionally by inserting the fangs into the door. Alternatively the animals hang upside-down in the burrows and pull on the door with the tarsal claws of the hind legs. Such positions are often observed when a door is prised slightly open.

Both species of *Anidiops* construct in the burrow a special device here referred to as a "sock". Essentially this structure is a loose tube or sock of silk, continuous at its lower extremity with the general lining of the burrow but at its upper limit being loosely connected by a few strands of silk to the burrow lining. This upper fimbriated part is always several inches below the burrow entrance. After feeding, this attachment is broken and food refuse is deposited in the space between the collar and the soil wall of the burrow, and the top of the collar or sock is then reattached to the upper silk lining. Upon disturbance at the burrow entrance the spider will retreat below the sock and, by pulling on it with palps and anterior legs, cause the attachment threads to break and the whole structure to collapse and become



Fig. 21.—Geographical distribution of *Aganippe cupulifex*, sp. nov., in Western Australia.

inverted. The appearance from above of a collapsed sock is that of the bottom of an ordinary trapdoor burrow, i.e. a heap of food remains. That the sock is a defence mechanism is clearly demonstrated when a section of a burrow is made in the field. It often happens that the whole burrow lining can be exposed unbroken from one side. If a slit is then made in the silken wall one can observe the animal, in profile, pulling down the sock. Its effectiveness against predators has been observed in the field and recorded previously (Main 1956). Such efficacy is also recorded in Table 10. The structure of the sock is shown diagrammatically in Figures 23B–23D.

The specialized defence behaviour of *I. nigrum* is to assume a phragmotie position in the burrow, plugging a narrow section with the truncated posterior portion of its abdomen. If the animal is disturbed when in a feeding attitude it will simply somersault and drop into a phragmotie position (Plate 6, Fig. 3). Tapping the hard sclerotized abdomen with a pencil elicits a clicking sound, but tapping and even pushing will not budge an animal. The position may be maintained for about an hour.

TABLE 10
 INSTANCES OF PREDATION ON AGANIPPINES BY ISOMETROIDES VESCUS (KARSCH) AND
 CORMOCEPHALUS SP.

Predator	Prey Species	Western Australian Localities	No. of Observed Instances	Notes
<i>I. vescus</i> (scorpion)	<i>Eucyrtops latior</i> (?)	Newdegate	1	Spider destroyed, scorpion with distended abdomen
	<i>Anidiops manstri-dgei</i>	Magooinya	1	Scorpion above, spider below sock
	<i>An. villosus</i>	Minnivale	1	Scorpion above, spider below sock
	<i>An. villosus</i>	Lake Kirk, 8 miles S. of	1	Scorpion with distended abdomen, fresh remains of spider in burrow (observed by A. R. Main)
	<i>An. villosus</i>	Cardinia Ck.	1	Spider dead and shrivelled below sock, cast of scorpion above sock (observed by A. R. Main)
	<i>Aganippe cupulifex</i>	Bungulla, 9 miles N. of	1	Spider destroyed, scorpion's abdomen greatly distended, with cast and spider remains at bottom of burrow
	<i>Ag. cupulifex</i>	Mt. Dick	1	Spider destroyed
	<i>Ag. cupulifex</i>	Newdegate	1	Spider destroyed
	<i>Ag. raphiduca</i>	Mullewa	1	Spider destroyed, scorpion with distended abdomen
	Proto- <i>Idiosoma</i> race (?)			
	Twig-lining race	Bulong, 5 miles SE. of	1	Spider destroyed
	<i>Ag. occidentalis</i>	Merkanooka	2	Scorpions feeding on spiders
	<i>Ag. occidentalis</i>	Peak Charles	4	Spiders destroyed
<i>Cormocephalus</i> sp. (centipede)	<i>Ag. raphiduca</i> , proto- <i>Idiosoma</i> race, or <i>I. nigrum</i>	Flint Gully	1	Spider destroyed
<i>Cormocephalus</i> sp.	<i>An. manstridgei</i>	Magooinya	1	Fresh remains of spider in burrow with centipede
<i>Cormocephalus</i> sp. (?) (specimen damaged while collecting)	<i>Ag. raphiduca</i> , proto- <i>Idiosoma</i> race, or <i>I. nigrum</i>	Pintharuka	1	Spider destroyed

Presumably this attitude is a general defence measure, partly associated with the fact that a thin wafer door is of little defence value, collapsing under strain.

It is of interest that three other unrelated trapdoor spiders, *Galeosoma schreineri* Hewitt, from South Africa, *Cyclocosmia truncata* (Hentz), and *Chorizops loricatus* (C. Koch), both North American species, which have also sclerotized and truncated abdomens, exhibit a similar phragmotic habit to that of *I. nigrum* (Hewitt 1923; Gertsch and Wallace 1936). These authors postulate that the behaviour is a defence against wasps. The attitude of *Idiosoma* does not necessarily protect them from ectoparasitic wasps since a parasitized burrow has been observed (Table 11).

TABLE 11
INSTANCES OF PARASITISM OF AGANIPPINES BY ECTOPARASITIC WASPS

Species Parasitized	Life-history Stage of Parasite	Western Australian Localities	No. of Specimens
<i>Eucyrtops latior</i>	Intact pupa	Albany Highway, 164 mile peg	1
<i>Anidiops villosus</i>	Empty pupal shell	Minnivale	1
<i>Aganippe occidentalis</i>	Empty pupal shells	Mt. Ragged, 10 miles SE. of	2
<i>Ag. cupulifex</i>	Intact pupa, adult wasp since emerged in laboratory	Walebing, 5 miles E. of	1
<i>Ag. cupulifex</i>	Larvae	Avon Valley, near Jimperding Hill	2
<i>Ag. cupulifex</i>	Intact pupa*	Avon Valley, near Jimperding Hill	1
<i>Ag. cupulifex</i>	Empty pupal shell	Bendering, 5 miles W. of	1
<i>Ag. cupulifex</i>	Empty pupal shell	The Humps, Hyden	1
<i>Ag. cupulifex</i>	Empty pupal shell	Emu Hill (near Narembreen)	1
<i>Ag. raphiduca</i>			
Type race	Empty pupal shells	Churchman's Brook	2
Type race	Empty pupal shell	Connelly Gully	1
Type race	Intact pupa	Near Waranine Gully	1
Twig-lining race	Intact pupa	Sandstone, 9 miles W. of	1
<i>Idiosoma nigrum</i>	Intact pupa	The Wongan Hills	1

* Several empty pupal shells also observed at this locality.

(h) Predators and Parasites

(i) *Predators*.—There is field evidence that scorpions, centipedes, and birds all prey on trapdoor spiders in their burrows. Scorpions and centipedes have been discovered feeding on the bodies of spiders in their burrows (Table 10). The magpie (*Gymnorhina dorsalis* Campbell) has been observed feeding on specimens of *Ag. cupulifex* at The Humps, Hyden. The magpies were pecking at the animals while in a foraging position at the top of the burrow. At least the soft abdomens were eaten by the birds while the battered cephalothorax and legs were left lying on the ground beside the torn-off doors and burrow rims. Torn-out tops of burrows are frequently

observed in the bush. One female specimen of *E. latior* has been found in the gut of the frog *Heleioporus australiacus* (Shaw).

(ii) *Parasites*.—Ectoparasitic wasps have been observed parasitizing aganippines. Recorded instances are presented in Table 11.



Fig. 22.—Geographical distribution of the species of *Idiosoma* Ausserer in Western Australia.

(i) *Feeding Biology*

(a) *Food Preferences*.—The Aganippini usually deposit their food refuse at the bottom of the burrow. In burrows of old animals, pockets of such debris, marking the earlier lower limits of the burrow, also occur along the walls. This rejectamenta often contains identifiable fragments. It is intended later to present a more detailed account of the food preferences when the material has been thoroughly studied. From a cursory examination of the debris the spiders can be classified arbitrarily into three groups as follows: beetle feeders, generalized feeders, and ant feeders. The type of prey taken is probably governed largely by the type of habitat occupied by the spiders. Thus, as a generalization, dwellers under litter seem to feed almost exclusively on beetles, animals occupying riparian and open situations (e.g. claypans

and lightly littered areas) are generalized feeders (beetles, ants, various insects and other arthropods, annelids, and other small invertebrates), and finally linear litter dwellers, which are usually twig-liners, are essentially ant feeders.

In some environments it is possible to observe the levels in the food chain. For instance in many of the linear litter environments the sequence is as follows: Scale insects (coccids) feed on the *Acacia* sap, ants feed on the coccids, and the trapdoor spiders feed on the ants. Such a habitat often provides little else for the spiders

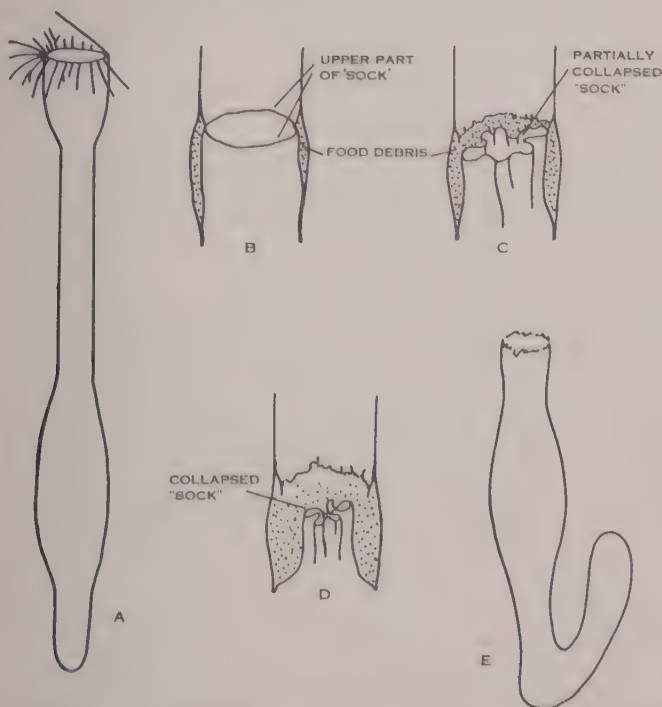


Fig. 23.—A, diagram of burrow profile of *Idiosoma* Ausserer. $\times c. \frac{1}{2}$; B, C, D, profile of top of "sock" in *Anidiops* Pocock burrow. $\times c. \frac{1}{2}$; E, bottom of burrow of a specimen of *Aganippe raphiduca* Rainbow & Pulleino, twig-lining race. $\times c. \frac{1}{2}$.

but ants. This partly accounts for dense aggregations of spiders around the base of mulga (*A. ancura*) and jam (*A. acuminata* and *A. burkittii*) trees when these trees form a pure stand. The litter zone provides the twigs which are utilized by the spiders as forage lines, and it is across this area that the ants pass in hordes to the trunks of the trees. Between the trees the ant movements are more diffuse.

(ii) *Foraging Behaviour and Its Relation to Habitat.* Briefly the relationship of feeding behaviour to habitat is as follows: Generally, species occurring in any type of habitat except situations of linear litter (e.g. dense spatulate litter and open sites), retain a generalized feeding method, i.e. with the burrow lacking any prey-searching appurtenances (exceptions are twig-lining forms of *Ag. raphiduca* and *cupulifex* and some populations of *An. villosus* in spatulate or mixed litter).

Conversely all species in linear litter situations exhibit the twig-lining foraging adaptation (exceptions are *E. latior*, which occasionally occurs under a dense mat of *Casuarina* litter, and *E. eremaea* collected from beneath *A. aneura* litter; these forms, so far as is known, forage beneath, not above, the litter stratum).

When foraging, animals have the tarsi of the palps and anterior legs resting on the rim of the burrow with the door slightly ajar. Each anterior tarsus of a twig-lining animal is in contact with an individual forage line where it is attached to the burrow rim. Animals which forage within the litter stratum probably detect

TABLE 12
PRINCIPAL FORAGING METHODS EMPLOYED BY AGANIPPINE SPECIES IN RELATION TO TYPE OF
HABITAT OCCUPIED

Species	Non-twig-lining Species: Never Completely Emerge from Burrow		Twig-lining Species: Completely Emerge from Burrow
	Sight not Involved in Perceiving Prey (?)	Sight Involved in Perceiving Prey (?)	Prey Detected by Tarsi and then by Eyes (?)
	Animals Forage within Litter Strata	Animals Forage above Litter Strata or in Open Sites	Animals* Forage above Litter Strata
<i>Eucyrtops latior</i>	+	—	—
<i>E. eremaea</i>	+ (?)	—	—
<i>E. riparia</i>	—	+	—
<i>Anidiops manstridgei</i>	+ (?)	+	+
<i>An. villosus</i>	—	+	+
<i>Aganippe subtristis</i>	+ (?)	+ (?)	—
<i>Ag. smeatoni</i>	—	+	—
<i>Ag. occidentalis</i>	—	+	+
<i>Ag. raphiduca</i>	—	+	+
<i>Ag. cupulifex</i>	—	+	+
<i>Idiosoma sigillatum</i>	—	—	+
<i>I. nigrum</i>	—	—	+

* Burrows found amongst linear litter or sometimes spatulate or mixed litter.

prey partly through the cephalic bristles which are in contact with the flimsy litter door. Those in open situations appear to be able to see movements outside the burrow. Initial perception of prey by twig-lining animals appears to be wholly tactile, since, when in a foraging posture the eyes are directed to the hinge wall of the burrow (at least in *Idiosoma* burrows which have a vertical entrance (see Fig. 23A) instead of an inclined one typical of the other aganippines). However, once such animals have emerged on to the forage lines they probably have a wide visual range.

Most trapdoor spiders do not completely emerge from the burrow when capturing prey, thus their area of search is restricted to a small semicircle in front of

the burrow, with radius of only as far as the spider can reach while still half within the burrow. However, twig-lining animals completely emerge and run out along the twig lines. Thus, with the attachment of twig lines, some of which may be up to 8 and 10 in. in length, the spider greatly increases its area of search for food. The adaptive value of such a behaviour pattern in semi-desert habitats is easily appreciated. This sort of behaviour has its parallel in other groups of spiders which have silken trap lines radiating from their burrow openings (e.g. the genus *Ariadna*, family Segestriidae). The dominant foraging methods in relation to habitat of the various species is stated in Table 12.

V. MORPHOLOGY AND BEHAVIOUR

(a) *Morphological Trends (adaptive characters)*

Of the females and juveniles, the characters which show the greatest degree of adaptive modification are: shape of the caput, size and distance apart of the eyes, number and length of cephalic bristles, relative length and thickness of the legs, and degree of sclerotization of the abdomen.

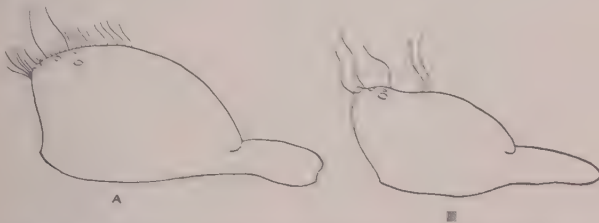


Fig. 24.—Profile aspects of carapaces of aganippines. *A*, *Eucyrtops latior* (Cambridge) (B.M. 52/77); *B*, *Idiosoma nigrum* Main (B.M. 53/88).

(i) *Shape of the Caput*.—In what appears to be the basic or least modified type of aganippine caput, the profile exhibits a pronounced upward slope from the clypeus to the area behind the eyes. Thus the highest part of the caput is the region between the ocular area and the fovea. The eyes are spread out on this upward sloping area and vision is directed entirely to the front.

The general trend in the tribe is for the caput to become depressed. The two extreme conditions of the caput slope, as represented by *E. latior* ("primitive" condition) and *I. nigrum* ("advanced" condition) are shown in Figures 24*A* and 24*B*.

(ii) *Eyes*.—The general trend in the eye arrangement is increase in size, correlated with a reduction of the interocular spaces. Generally, the total ocular area relative to the width of the caput appears to be approximately the same for all species. Variation exists not only between species but also adaptively within species.

The general trend for enlargement and approximation of the eyes is illustrated in Figure 25. Representative diagrams of all species are here depicted in a comparative way. This is intended to represent the range of variability for each species but not necessarily the total number of variations.

(iii) *Cephalic Bristles*.—The caput has a characteristic group of bristles associated with the eyes and sometimes extending posteriorly to the fovea. There appears to be a general trend for reduction in number of these bristles.

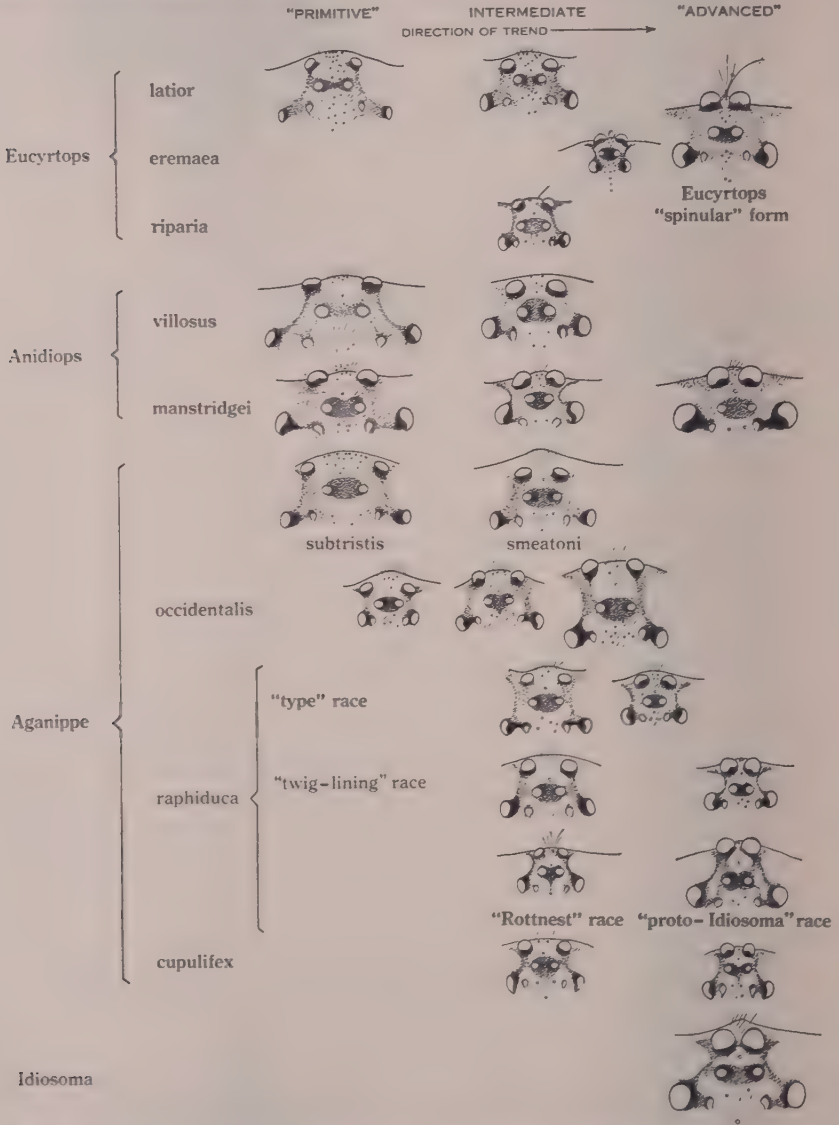


Fig. 25.—Range of adaptive variation of eye arrangement of aganippine species. / c. 5.

The site of the cephalic bristles is indicated in the figures showing the characteristic eye arrangements for the various species (Fig. 25). Bristles are also shown in profile in Figures 24A, 24B.

(iv) *Legs*.—The legs show a general trend towards elongation and correlated decrease in thickness from the primitive condition of relatively short stout legs. This is a specialized problem requiring a particular analysis not yet completed. It appears to be one of the more complicated evolutionary trends of the group.

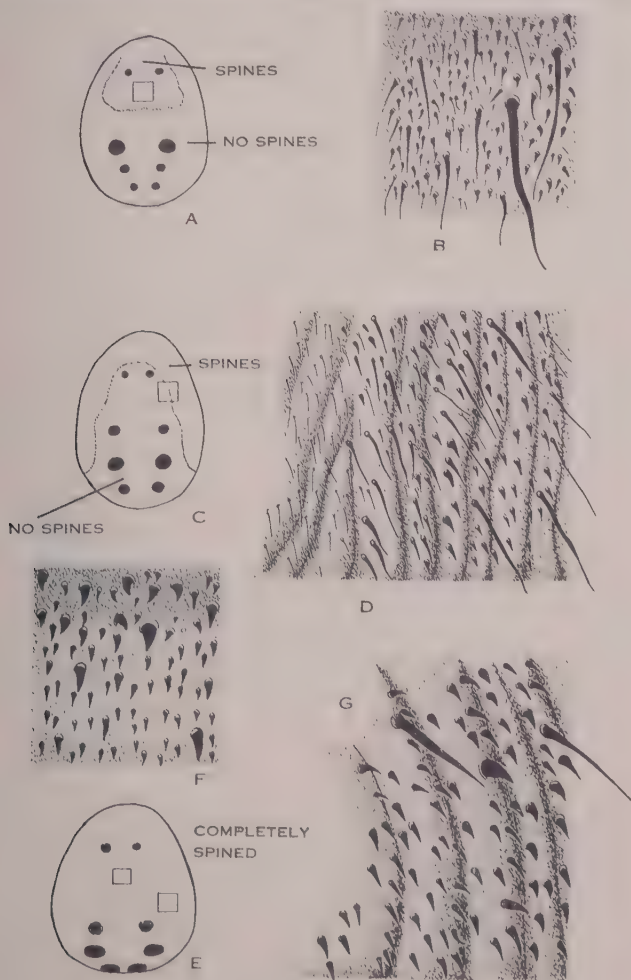


Fig. 26.—Sequence in trend for abdominal spination in *Aganippe raphiduca* Rainbow & Pulloine. *A, B*, simplest level of spinianness (B.M. 53/261); *C, D*, slightly more advanced condition: note incipient lateral corrugations (B.M. 53/364). *E, F, G*, most advanced condition, abdomen completely spiny: note incipient corrugations (B.M. 54/279).

Due to specific functions of the particular legs, modification of one leg is not necessarily correlated with modification of another.

(v) *Sclerotization of the Abdomen*. The approximate sequence of increasing sclerotization of the integument, as indicated by the dorsal abdominal cuticle, is:

- (1) Development of an anterior and a median pair of sigilla;
- (2) Development of 2 posterior pairs of sigilla;
- (3) Appearance of median anterior spines or lateral spines or both (shown in Figs. 26A-26D);
- (4) Spines may extend posteriorly (very rarely spines also develop ventrally);
- (5) Posterior sigilla enlarge and anterior 2 pairs degenerate;
- (6) Appearance of incipient corrugations (shown in Figs. 26D, 26G);
- (7) Posterior truncation (Figs. 27A-27C);
- (8) Corrugations become pronounced (latero-longitudinal and posterior-transverse);
- (9) Dorsum becomes scute-like and inflexible (Figs. 2G, 2H).

TABLE 13

THREE DOMINANT LEVELS OF ADAPTIVE MORPHOLOGY AND DIRECTION OF TREND OF MODIFICATION

Without abdominal sigilla		With abdominal sigilla	
<i>Eucyrtops latior</i> <i>E. eremaea</i> (except eyes) <i>Anidiops manstridgei</i> (eyes only)	High caput, small widespread eyes, many cephalic bristles, short stout legs	<i>Aganippe subtristis</i>	2 pairs sigilla
↓			
<i>E. riparia</i> <i>E. latior</i> (some characters) <i>An. manstridgei</i> <i>An. villosus</i>	Moderately depressed caput, moderately enlarged eyes, fewer cephalic bristles, slightly longer and thinner legs	<i>Ag. occidentalis</i> <i>Ag. smeatoni</i> <i>Ag. raphiduca</i> <i>Ag. cupulifer</i>	2-4 pairs sigilla, slight tendency for spininess
↓			
<i>An. manstridgei</i>	Depressed caput, grossly enlarged approximated eyes, few cephalic bristles, long slender legs	<i>Ag. raphiduca</i> , proto- <i>Idiosoma</i> race <i>Idiosoma sigillatum</i> <i>I. nigrum</i>	4 pairs sigilla, usually heavy spination and tending to cor- rugations

It would appear that development of the 2 anterior pairs of sigilla has occurred only once in the history of the tribe and that there has subsequently occurred parallel accentuation of the condition of thickening of the integument, as evidenced by the independent spinular development in at least four species of *Aganippe*.

(b) Correlation of Morphological Trends

There is a parallel trend of correlated morphological features, excepting with regard to the abdominal sclerotization in the two natural subgroups of the tribe. These associated trends are summarized in Table 13.

(c) *Trends in the Structure of the Male External Genitalia*

Differences in structure of the male palp and apophyses of the first tibia are generally regarded as external indication of reproductive isolation between species. There are two dominant trends in the modification of these parts represented by the two generic groups. These trends are shown in Table 14 and Figure 28.



Fig. 27.—Sequence in levels of abdominal truncation in *Aganippe raphiduca* Rainbow & Pulleine: *A*, representing the most "primitive" level, and *C*, the most "advanced".

(d) *Correlation of Morphology and Behaviour*

Burrow structure, foraging behaviour, and morphology are all closely associated with habitat. Within the tribe there appear to be three dominant phases in a general one-directional trend. The suggested comprehensive trend is presented in Table 15.

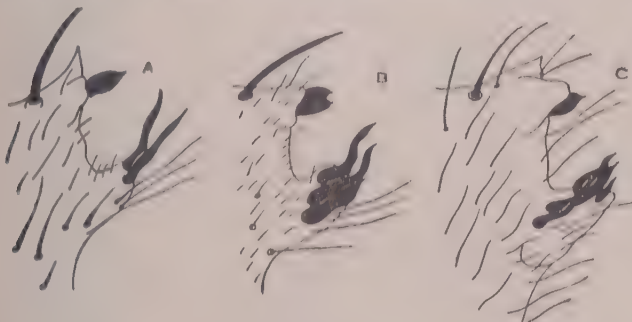


Fig. 28.—Ventral aspects of tibial apophyses on right legs (I) of male aganippine specimens: *A*, condition found in many specimens of *Aganippe subtristis* (Cambridge) and some little-modified specimens of type race of *Ag. raphiduca* Rainbow & Pulleine and *Ag. cupulifex*, sp. nov.; *B*, a more "advanced" condition found in some specimens of *Aganippe* Cambridge; *C*, the usual condition found in *Idiosoma* Ausserer.

VI. EVOLUTION

Spiders as an order were established by the middle Palaeozoic. Divergence into families, begun by the Carboniferous, continued through the Mesozoic and possibly into the Tertiary. At all events the Recent families were established not later than Miocene and many Recent genera were present in the Oligocene (Petrunkovitch 1953, p. 116). From this it seems reasonable to suggest that the ancestor of the Aganippini could have entered Australia during early Tertiary. Assuming that the proto-aganippine was not grossly unlike the more primitive present-day members of the group such as *E. latior*, and had similar environmental requirements, it can

TABLE 14
TRENDS IN MODIFICATION OF MALE PALP AND FIRST TIBIAL STRUCTURES

<i>Bucyrtops/Ancistrus</i> Lines (except <i>An. mansuetor</i>)		<i>Agavep/Idiosoma</i> Line	
Palpal Tibia	Stigma	Palpal Tibia	Tibia I
No processes (except Stirling Range specimens)	Short, bluntly pointed	Upper digital unspined process, median spined burr-like process	Long, tapering, pointed Double apophysis, few spines (Fig. 28A)
<i>E. riparia</i>		<i>Ag. subtristis</i> , <i>Ag. occidentalis</i> , and also <i>An. mansuetor</i>	
Upper group of spines, median spined apophysis	Short, bluntly pointed	Unspined digital and apophysis-like process	Strongly lateral twisted* flange† Double apophysis (except some <i>Ag. cupulifer</i>), few or many spines (Figs. 28A, 28B)
<i>E. latior</i> and <i>E. eremaea</i>		<i>Ag. emeatoni</i> *, <i>Ag. cupulifer</i> ,† and <i>Ag. raphiduca</i> †	
Upper and median spined apophysis	Short, bluntly pointed	Spines on upper digital process as well as on burr-like process	Greater latero-terminal elaboration Double apophysis, many spines (Fig. 28C)
<i>An. villosus</i>		<i>Ag. raphiduca</i> (proto- <i>Idiosoma</i> race) and <i>Idiosoma</i>	

be deduced that a habitat suitable for such an animal was probably available by early Oligocene when eucalypts, banksias, and hakeas were present (Chapman 1937). The Coleoptera, which comprise the dominant food item of the primitive aganippines, were already established as an order of insects at this time.

The pattern of speciation of the tribe Aganippini has been on a continent on which there are no conspicuous geographic barriers: thus the speciation cannot be attributed to fragmentation and isolation by geographic barriers such as mountain

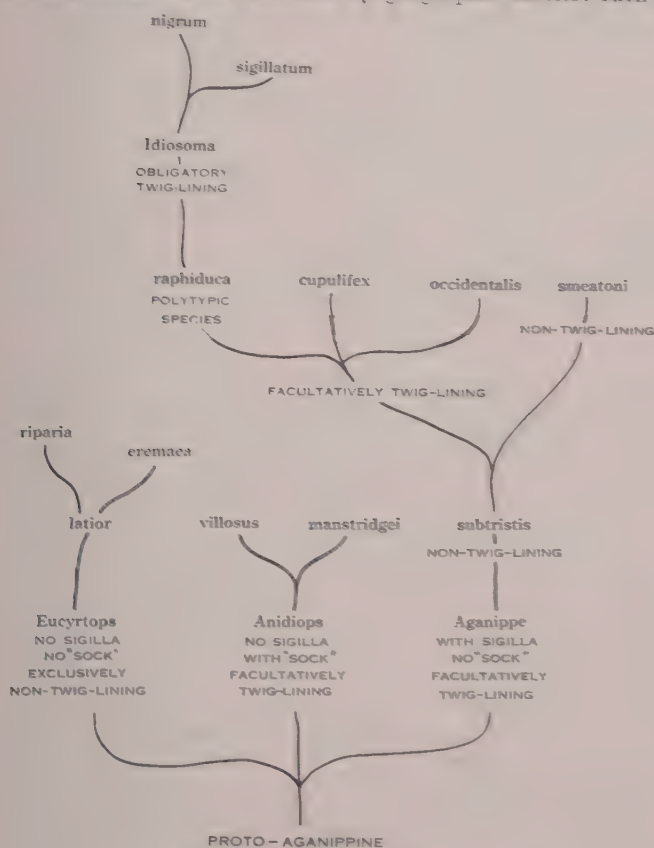


Fig. 29.—Suggested phylogeny of the Aganippini.

ranges. In effect, it appears that ecological factors, predominantly those associated with the availability of minor habitats, have contributed largely to the speciation of the group. Over this continental expanse the once widespread, probably uniform, population has responded differentially to the various localized environments, thus modification has developed around a number of "adaptive peaks" which have ultimately formed the geographical centres of origin of the present species. Subsequent periodic shifting of the areal limits of the environmental zones, possibly due to slight climatic fluctuations, has resulted in spatial overlap and admixture of

many of the species as they are now observed. A postulated phylogeny of the tribe is outlined in Figure 29.

The following account of the possible derivation of the various lines of the postulated phylogeny of the tribe, based on the foregoing observations, is presented with the reservation of being, in part, purely speculative.

The phylogenetic relationships have probably been attained by three main steps in sequence as follows:

- (1) Geographical fragmentation of an old west-east cline into three genera *Eucyrtops*, *Anidiops*, and *Aganippe*.
- (2) Geographical expansion of the genus *Aganippe* followed by ecological specialization of allopatric populations (speciation), with a parallel ecological expansion of *Anidiops* and *Eucyrtops* (speciation in *Eucyrtops* only).
- (3) A major ecological shift within the genus *Aganippe*, i.e. adoption of twig-lining, resulting in the new genus *Idiosoma* (this shift paralleled to a lesser degree in *Anidiops*).

These evolutionary steps are outlined below.

(a) *First Phase of the Radiation*

The least-modified morphological forms of the three species (*latior*, *manstridgei*, and *subtristis*) have also retained what is presumed to have been the primitive adaptive level, adaptation to a habitat of dense sclerophyllous litter. Thus it could be that these species represent the relicts of an ancient cline subsequently fragmented. Such a fragmentation could have occurred during the Miocene, when the engulfing seas could have partially fragmented a widespread southern population about three principal centres as follows: south-western Western Australia to as far east as Coolgardie and Norseman (*Eucyrtops*); a central block in the form of an arch from about the Fraser Range, curving north around the Nullarbor Plain and down to Eyre Peninsula (*Anidiops*); and finally, the Flinders Range (*Aganippe*).

The country east of the Flinders Range and along the Murray R. system is composed of marine sediments of Middle Tertiary age. The area occupied by these rocks indicates that the duration and extent of this marine transgression was such that the early radiation of the Aganippini would have been restricted to the Flinders Range and continental areas to the west.

(b) *Second Phase of the Radiation*

The dominant feature of the second major phase in the radiation of the tribe was probably associated with a westward geographical expansion of the *Ag. subtristis* stock. *Aganippe* probably originated as the eastern extremity of an old cline rather than having been present in the west concurrently with *Eucyrtops*. Following a westward movement of *Aganippe*, such a stock could then have diverged ecologically and broken into more or less distinct allopatric races, now represented by the species *raphiduca*, *cupulifer*, and *occidentalis*. *Ag. smeatoni* probably represents an analogous and simultaneous eastward expansion of the same basic *subtristis* stock. These four later-derived species probably developed as races adapting to open situations in

distinction to the primitive litter-type habitat. The new habitat occupied was that of either a riparian or claypan situation, and the new adaptation a combination of a door structure resistant to periodic sheet flooding and foraging in an open site. This ecological shift in the genus *Aganippe* was paralleled by the two species of *Anidiops* and *E. riparia*. The expansion of *Aganippe* probably occurred during early Pliocene. The speciation was most likely initiated during mid-Pliocene and the process is still continuing today. The ecological radiation of the genus *Aganippe* has clearly been in response to climatic and environmental conditions not

TABLE 15
RELATIONSHIP OF MORPHOLOGY AND BIOLOGY OF AGANIPPINE SPECIES

Biology	Morphology
<i>Habitat</i>	High upward sloping caput (except <i>An. manstridgei</i>), small widespaced eyes (except <i>E. eremaea</i>), numerous cephalic bristles, short stout legs
Vegetation formation which provides for a permanent layer of litter which completely obscures soil (usually a forest, woodland, or mallee association—exception is dense mulga litter along creeks, frequented by <i>E. eremaea</i>)	
<i>Burrow</i>	
With inclined entrance and loosely constructed door of litter fragments (except <i>E. eremaea</i> which has solid soil door)	
<i>Foraging</i>	
Forages at burrow entrance without emerging from burrow and remains completely within litter strata. Diet principally of litter-crawling beetles	
<i>Suggested Function</i>	
1. High caput throws line of vision to the fore; animal, by never emerging completely from burrow, unable to see in any other direction 2. Dense cluster of cephalic bristles presumably supersedes function of eyes in detecting presence of prey amongst litter 3. Short stout legs adapted for supporting and moving of animal in burrow which it never vacates 4. Fragile litter door merely obscures and protects opening; heavy soil door of <i>E. eremaea</i> prevents flooding of burrow	
<i>Examples</i>	
<i>E. latior</i> , <i>E. eremaea</i>	
<i>An. manstridgei</i> (from Eyre Peninsula, S.A.)—with depressed caput	
<i>Ag. subtristis</i>	
Behaviour of <i>An. manstridgei</i> and <i>Ag. subtristis</i> inferred from comparison of morphology and correlated burrow structure of <i>E. latior</i>	

greatly unlike those experienced today although the geographical limits of such regions were probably not completely coincident with those of today. It is probable that the Pliocene climate of south-western Australia was of this Mediterranean nature. This is supported by the fact that Axelrod (1948) has shown that areas of similar latitude to south-western Australia, namely south-western North America, portions of Europe and Asia, and in South America, parts of Chile, Argentina, and Patagonia had a warm arid Pliocene climate.

TABLE 15 (Continued)

Biology	Morphology
<i>Habitat</i> Riparian situations or areas of bare ground or at most with light drifting litter, never with stable litter zone (usually a eucalypt woodland association)—areas which are subjected to periodic flooding	Moderately depressed caput, moderately enlarged eyes, relatively fewer cephalic bristles, slightly longer and thinner legs
<i>Burrow</i> With inclined entrance; soil door usually a solid structure which is so hinged as to open only to an acute angle not exceeding about 45°. Flap-like door in riparian situations, cork-like in claypans	
<i>Foraging</i> Forages at buttow entrance, never completely emerging. Forages in open site unobscured by litter. Diet mixed, includes ants	
<i>Suggested Function</i>	
1. Moderately depressed caput directs eyes laterally and posteriorly as well as anteriorly; this, combined with the partly enlarged eyes, makes vision more efficient, which is of advantage since, although the animals do not vacate the burrow, they must detect prey by sight in the open environment	
2. Eyes more important for detecting prey than cephalic bristles which are reduced in number	
3. Slightly longer, thinner legs, more efficient for seizing fast-moving prey (e.g. ants), also probably allows for greater emergence or extension from burrow while seizing prey. Heavy soil door, opening acutely, precludes complete emergence from burrow; cork-like door able to withstand flooding	
<i>Examples</i> <i>E. riparia</i> <i>An. villosus</i> (in part), <i>An. manstridgei</i> (in part) <i>Ag. occidentalis</i> <i>Ag. raphiduca</i> , type and Rottneest races <i>Ag. cupulifex</i> , western populations <i>Ag. smeatoni</i> (from Mt. Lofty Ranges, S.A.)—behaviour inferred from morphology and burrow structure	

Attainment of reproductive isolation between the various forms of *Aganippe* may have been the result of selection operating along geographic lines of contact, by eliminating hybrids, i.e. by favouring any modifications (such as of male structures) which might tend to prevent cross breeding and thereby maintain the adaptive genotypes. Such a mechanism was suggested by Dobzhansky (1941, pp. 285-6) as

TABLE 15 (Continued)

Biology	Morphology
<i>Habitat</i>	Depressed, posteriorly sloping caput, eyes moderately to grossly enlarged and approximated, cephalic bristles reduced in number but elongated, legs tending to become longer and thinner
Stable litter, usually linear. Principally "islands" of <i>Casuarina</i> or <i>Acacia</i> in forest and woodland formations or mulga zone	
<i>Burrow</i>	
Rim with attached twig lines. Entrance tending from being slightly inclined to vertical (vertical entrance facilitates door standing open at 90°). Soil door opens to 90° but will not stand open unpropped	
or	
Door principally of litter material, very lightweight, and so hinged that it stands open without propping	
<i>Foraging</i>	
Animal throws open door and runs out along twig lines to capture prey, thus frequently entirely vacates burrow	
<i>Suggested Function</i>	
1. Depressed caput directs eyes in all directions, related to fact that animal completely vacates burrow when feeding 2. Enlarged approximated eyes give better vision; associated with twig-lining foraging behaviour where animal detects prey at a distance 3. Elongation of cephalic bristles gives more refined sensitivity (?) 4. Elongated slender legs adapted for running rapidly on horizontal plane (e.g. along twig lines outside the burrow) 5. Lightweight door which opens to wide angle and often stands open unsupported of advantage when animal completely emerges when pursuing prey along twig lines	
<i>Examples</i>	
<i>An. villosus</i> (in part)—twig door but morphological level not extreme	
<i>An. manstridgei</i> (in part)—twig door and extreme morphological level	
<i>Ag. occidentalis</i> , <i>Ag. cupulifer</i> , and <i>Ag. raphiduca</i> (in part)—soil doors and morphology only moderately accentuated	
<i>Ag. raphiduca</i> , twig-lining race—twig door, morphology of northern population moderately accentuated, southern forms extreme	
<i>Ag. raphiduca</i> , proto- <i>Idiosoma</i> race—twig door, morphology tends to extreme	
<i>I. sigillatum</i> , <i>I. nigrum</i> —extreme behaviour for burrow structure and morphology	

follows: "... the genotype of a species is an integrated system adapted to the ecological niche in which the species lives. Gene recombination in the offspring of species hybrids may lead to the formation of individuals with discordant gene patterns, the destruction of which entails a decrease of the reproductive potentials of the species whose members interbreed."

Both *Anidiops* and *Eucyrtops* also exhibit a parallel adaptation to open situations. Both species of *Anidiops* are frequently found in areas of sheet flooding. Although *An. manstridgei* primarily inhabits areas of dense sclerophyllous litter, so that adaptation to open situations such as clay flats on the Nullarbor Plain represents an ecological shift, such populations do not appear to be reproductively isolated. *Eucyrtops*, however, by expanding into a riparian situation, has developed another species, *riparia*. Also the geographic isolate *E. cremata*, has almost certainly been derived from the basic *latic* stock. The status of the "spinular" form cannot yet be stated.

(c) Third Phase of the Radiation

The third phase in the evolution of the Aganippini has been the adaptation, by means of twig-lining to semi-desert conditions. By adopting the twig-lining method of foraging, animals increase their area of search. This adaptation has shown a parallel development in the genera *Aganippe* and *Anidiops*. In the two species of *Anidiops* behavioural plasticity has been retained (i.e. they continue to exist in the former habitats of dense sclerophyllous litter and areas of sheet flooding as well as having some populations adapted to drier habitats). Populations occupying the various habitats appear to be reproductively continuous. Likewise, some species of *Aganippe*, such as *cupulifer* and *occidentalis* which have adopted the twig-lining behaviour, are still continuous with non twig-lining populations and certain populations show genetic admixture of the two behavioural levels, as do also certain of the *Ag. raphiduca* populations. This is apparent since broods taken from sites which exhibit both behavioural types, when returned to the laboratory and given equal opportunity to twig-line, segregate into twig-lining and non-twig-lining groups, i.e. within the one brood both behavioural patterns are found.

The morphological and biological characteristics of the four races of *Ag. raphiduca* are summarized in Table 7. Presumably the four races of this complex have been derived from a once widespread population which has responded adaptively to localized environmental influences. The relationship of the distribution of the adaptive forms to the available habitats is shown in Figure 20.

The intermediate populations of the type and proto-*Idiosoma* races demonstrate the origin and evolution of a new adaptation. These intermediate populations exhibit many combinations of the various morphological and behavioural characters. Twenty-one different combinations of the more readily classifiable characters, namely eyes, stigma, abdominal spaces, door structure, presence or absence of twig lines, and inclination of the burrow entrance have been observed (see Table 16). Plate 1, Figure 4 illustrates a burrow entrance of an intermediate animal, showing an insect soil door but with twig lines on the burrow rim.

From the zone of adaptive intermediacy, 59 specimens have been collected but complete data are available for only 46. These specimens represent samples from 23 populations and the maximum number of specimens in any one sample is seven. Only nine of the 23 population samples contain at least two specimens with complete data. The number of different combinations found in each of these nine samples is shown in Table 17.

The above characters selected for analysis are somewhat arbitrary. Actually there is a gradation between *Aganippe*-like and *Idiosoma*-like eyes, degree of abdominal spination, burrow inclination, in the type of door, and number of twig lines which it has not been possible to indicate in this preliminary report. Also, other features, including relative leg length need to be considered. However, in this initial investigation of the problem it has seemed best to make such categories as simple as possible. A more detailed analysis will be made later.

TABLE 17

SAMPLES FROM POPULATIONS INTERMEDIATE BETWEEN THE TYPE AND PROTO-IDIOSOMA RACES OF *AGANIPPE* RAPHIDUCA, CONTAINING AT LEAST TWO SPECIMENS, SHOWING LOCALITIES, NUMBER OF SPECIMENS FOR WHICH COMPLETE DATA ARE AVAILABLE, AND NUMBER OF DIFFERENT MORPHOLOGICAL AND BEHAVIOURAL COMBINATIONS IN EACH SAMPLE

Locality	No. of Specimens	No. of Combinations
Albany Rd., 112 mile peg	7	6
Popanyinning, 4 miles S. of	6	4
Brookton, 6 miles S. of	4	4
Brookton, 24 miles NW. of, on Kelmseott-Brookton Rd.	4	2
Katanning, 6 miles S. of	4	2
Bruce Rock, 13 miles N. of	2	2
Merredin, 5 miles N. of	2	2
Jilakin Rock, 5 miles N. of	2	1
Noongaar, 2 miles W. of	5	2

So far only small samples have been taken. In the future, should it be possible to take larger samples a greater range of character combinations may be found. It must be realized, though, that animals collected are usually at least two years old and probably selection by this time has already eliminated certain unfavourable combinations. Probably the genus *Idiosoma* has been derived either from a race of *Ag. raphiduca* or an earlier western twig-lining representative of the genus *Aganippe*, simply by accentuation of the twig-lining behaviour followed by ultimate fixation of such behaviour and concomitant morphology. The specimens of what were described as *I. hirsutum* (Main 1952) are now interpreted as being probably hybrids between the proto-*Idiosoma* race of *Ag. raphiduca* and *I. sigillatum* because of the intermediate morphology (i.e. with abdominal spines like an extreme form of the proto-*Idiosoma* race but with also distinct corrugations like *I. sigillatum* as shown in Fig. 15). However, evidence for such hybridization is slight and the geographical distribution for the most part does not permit it.

It seems that the characters which are assorting independently in *Aganippe* are inherited as a "block" in *Idiosoma*.

Simpson (1953, p. 347) emphasizes the significance of adaptive shifts in relation to the origin of higher categories. He discusses block inheritance in relation to origin of higher categories as follows: "It is even more common for "blocks" of characters (Mayr's phrase) than for single characters to be involved in the rise of higher categories. When they are and when the blocks tend to be retained as such, the simple explanation is that the block as a whole, its combination of characters, has adaptive value different from or additional to that of the various separate characters." This certainly appears to be so in regard to *Idiosoma* in contrast to such species as *Ag. raphiduca* which exhibits marked variability in the character combinations when occurring in the mixed-habitat region where presumably the selection for twig-lining fluctuates considerably from one locality to another, and from season to season. However, with *Idiosoma* selection must have operated exclusively at least for a time for the twig-lining adaptive extreme, in which case a block inheritance of the extreme characters would have been selectively favoured.

Finally, edaphic factors also appear to have a contributing influence on the ecological isolation of *Ag. raphiduca*, *cupulifex*, and *occidentalis* and *Idiosoma*. Throughout the sclerophyllous woodlands, sinuous belts of yellow sands, alternating with regions of loams and clays, appear to some extent to partially fragment and isolate many of the populations. Such fragmentation is believed to have played some part in the speciation of the group but distribution in relation to edaphic factors requires more detailed field study.

VII. ACKNOWLEDGMENTS

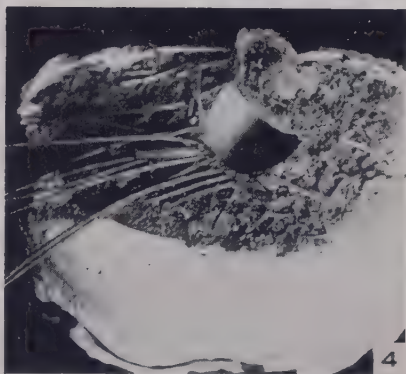
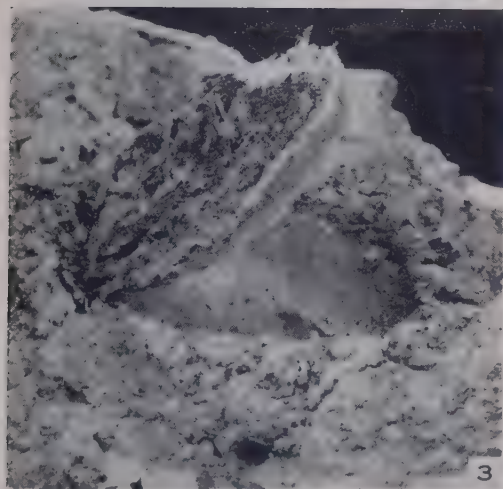
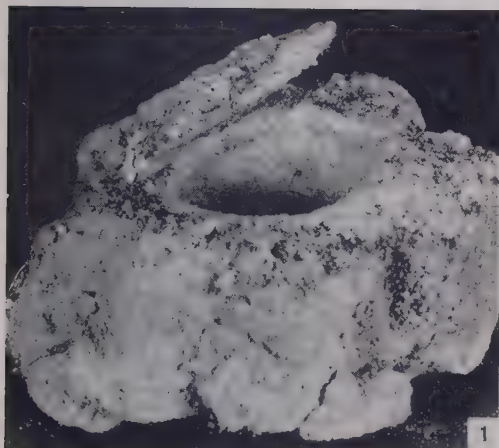
This work was done while in receipt of a University of Western Australia Research Grant. Assistance towards travel expenses was received from the Commonwealth Scientific and Industrial Research Organization. Thanks are due to the following: Dr. J. W. Evans, Director, and Mr. A. Musgrave, Curator of Insects and Arachnids, Australian Museum, Sydney, for facilities in the museum and opportunity to examine type material; Mr. R. T. M. Pescott, Director, Mr. A. N. Burns, Entomologist, and Messrs. R. A. Dunn and L. S. G. Butler, Honorary Arachnologists, National Museum, Melbourne, for facilities and opportunity to examine mygalomorph specimens in the museum collection; Mr. H. M. Hale, Director, Mr. H. Womersley, Entomologist, and Mr. G. F. Grosse, Assistant Entomologist, South Australian Museum, for opportunity and facilities to examine type material and other specimens in the museum collection; Mr. G. Mack, Director, Queensland Museum, for permission to examine the collection of mygalomorph spiders in the museum; Mr. L. Glauert, Director, and Mr. A. Douglas, Entomologist, Western Australian Museum, for permission to examine the collection of Mygalomorphae in the museum. The author is indebted to Professor V. V. Hickman, Zoology Department, University of Tasmania, for sending a specimen of *Arbanitis tasmanica*. Mr. E. Walshe and Mr. V. N. Serventy took photographs as acknowledged in the Explanation of Plates. Several friends gave specimens to the author during the course of this study. The late Mr. H. Tarlton Phillips collected a male specimen of *Ag.*

subtristis from Ayers Rock, N.T., and Mr. W. Johnstone collected the *Aganippe* specimens from Thistle I., S.A., which localities the author has not visited. The following people who collected for the author and assisted in the field work are gratefully acknowledged: Dr. W. B. Malcolm, Messrs. A. K. Lee and W. H. Butler, and Dr. A. R. Main.

VIII. REFERENCES

- AUSSERER, A. (1871).—Beitrage zur Kenntniss der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). *Verh. zool.-bot. Ges. Wien* **21**: 117–224.
- AXELROD, D. I. (1948).—Climate and evolution in western North America during middle Pliocene time. *Evolution* **2**: 127–44.
- BAERG, W. J. (1945).—The black widow and the tarantula. *Trans. Conn. Acad. Arts Sci.* **36**: 99–111.
- CAMBRIDGE, O. P. (1877).—On some new genera and species of Araneidea. *Ann. Mag. Nat. Hist.* (4) **19**: 26–39.
- CHAPMAN, F. (1937).—Descriptions of Tertiary plant remains from Central Australia and from other Australian localities. *Trans. Roy. Soc. S. Aust.* **61**: 1–16.
- DELACOUR, J., and MAYR, E. (1945).—The family Anatidae. *Wilson Bull.* **57**: 1–55.
- DOBZHANSKY, T. (1941).—“Genetics and the Origin of Species.” (Columbia University Press: New York.)
- EVANS, H. E. E. (1953).—Comparative ethology and the systematics of spider wasps. *Syst. Zool.* **2**: 155–72.
- GARDNER, C. A. (1944).—The vegetation of Western Australia with special reference to the climate and soils. *J. Roy. Soc. W. Aust.* **28**: xi-lxxxvii.
- GERTSCH, W. J., and WALLACE, H. K. (1936).—Notes on new and rare American mygalomorph spiders. *Amer. Mus. Novit.* No. 884, pp. 1–25.
- HEWITT, J. (1913).—Descriptions of new and little known species of trapdoor spiders (Ctenizidae and Migidae) from South Africa. *Rec. Albany Mus.* **2**: 404–34.
- HICKMAN, V. V. (1927).—Studies in Tasmanian spiders. II. *Proc. Roy. Soc. Tasm.* **1927**: 158–75.
- HOGG, H. R. (1902).—On some additions to the Australian spiders of the sub-order Mygalomorphae. *Proc. Zool. Soc. Lond.* **1902** (2): 121–42.
- HOGG, H. R. (1903).—Two new Australian spiders of the family Ctenizidae. *Ann. Mag. Nat. Hist.* (7) **11**: 308–12.
- MAIN, B. (1957).—Adaptive radiation of trapdoor spiders. *Aust. Mus. Mag.* **12**: 160–3.
- MAIN, B. Y. (1952). Notes on the genus *Idiosoma*, a supposedly rare Western Australian trap-door spider. *W. Aust. Nat.* **3**: 130–7.
- MAIN, B. Y. (1956).—Taxonomy and biology of the genus *Isometroides* Keyserling (Scorpionida). *Aust. J. Zool.* **4**: 158–64.
- PETRUNKEVITCH, A. (1953).—Palaeozoic and Mesozoic Arachnida of Europe. *Mem. Geol. Soc. Amer.* **53**: 122.
- POCOCK, R. I. (1897).—On some trap-door spiders of the family Ctenizidae from south and west Australia, contained in the collection of the British Museum. *Ann. Mag. Nat. Hist.* (6) **19**: 109–16.
- PULLEINE, R. H. (1919).—A new species of *Aganippe* from Kangaroo Island. *Trans. Roy. Soc. S. Aust.* **40**: 74–6.
- RAINBOW, W. J. (1914).—Studies in Australian Araneidae—No. 6. The Terretelariae. *Rec. Aust. Mus.* **10**: 187–270.
- RAINBOW, W. J., and PULLEINE, R. H. (1918).—Australian trap-door spiders. *Rec. Aust. Mus.* **12**: 81–169.
- SIMON, E. (1892).—“Histoire Naturelle des Araignées.” (Librairie Encyclopedique de Roret: Paris.)
- SIMON, E. (1903).—“Histoire Naturelle des Araignées.” Supplément Général. (Librairie Encyclopedique de Roret: Paris.)
- SIMPSON, G. G. (1953).—“The Major Features of Evolution.” (Columbia University Press: New York.)

BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS



ECOLOGY OF ARGENTINE TREPONID SPIDERS



BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS



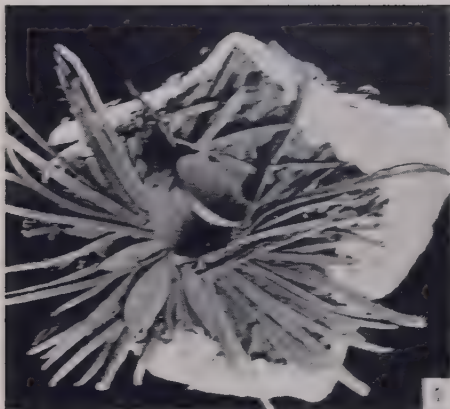
BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS



BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS



BIOLOGY OF AGANIPPINE TRAPDOOR SPIDERS



EXPLANATION OF PLATES 1-6

Photographs in Plates 1 and 4 except Fig. 3 taken by Mr. E. Wailes. Plate 4, Figure 3, from photographs taken in the laboratory by the author. All other photographs taken by Mr. T. N. Serventy.

PLATE 1

- Fig. 1.—Door and entrance of burrow of *Eucynops apicatus*, sp. nov. B.M. 54 565, from creek at base of Mt. Misery, W.A.).
- Fig. 2.—Door and entrance of burrow of *Apsopage confinis* Hogg B.M. 54 565, from 10 miles south-east of Mt. Ragged, W.A.).
- Fig. 3.—Door and entrance of burrow of *A. cephalotes* Rainbow & Pulleine, "type" race specimen from Brunswick Junction, W.A.).
- Fig. 4.—Door and entrance of burrow of *A. cephalotes* Rainbow & Pulleine, intermediate specimen between "type" and "prote-*Stictocera*" races B.M. 54 565, from 6 miles south of Brooklyn, W.A.).

PLATE 2

- Aggregate of burrows of *Apsopage raphiduca*, sp. nov. in riparian habitat at Wongamine, W.A. Doors show characteristic dome shape.

PLATE 3

- Fig. 1.—Entrance of twig-lining burrow, with door closed, of *Apsopage raphiduca*, sp. nov., at Boorabool, W.A. Dome shape of door is "depressed", characteristic for twig-lining specimens B.M. 55 405.
- Fig. 2.—The same burrow as in Plate 3, Figure 1, with the door propped open.

PLATE 4

- Fig. 1.—Entrance of burrow, with door closed, of "twig-lining" race of *Aganippe raphiduca* Rainbow & Pulleine, in spatulate leaf litter under eucalypts, 6 miles east of Coonana, W.A. B.M. 55 405.
- Fig. 2.—The same burrow as in Plate 4, Figure 1, with the door opened.

PLATE 5

- Fig. 1.—Entrance of burrow, with door closed, of twig-lining specimen of *Anidiops villosus* (Rainbow) in mixed spatulate-linear litter at Thomas R., W.A.
- Fig. 2.—The same burrow as in Plate 5, Figure 1, with door opened.

PLATE 6

- Fig. 1.—Entrance of burrow, with door open, of twig-lining specimen of *Apsopage confinis* Hogg, from Caversham, W.A.
- Fig. 2.—The same burrow as in Plate 6, Figure 1, with door closed, showing "dropped" attitude.
- Fig. 3.—*Stictocera raphana* Main B.M. 55 176 in phragmites position.

VARIATION AND SPECIATION IN THE GENUS *CLIMACTERIS* TEMMINCK (AVES: SITTIDAE)

By A. KEAST*

[Manuscript received July 22, 1957]

Summary

The present paper determines the status and range of forms in the genus *Climacteris* Temminck (tree-creepers) formerly regarded as species; it also reviews infraspecific variation, re-defines races, and is a detailed study of speciation in the genus.

Climacteris is a most interesting genus in the information it yields with respect to speciation. Forms occur that represent the full range of intermediate stages right up to the one that has demonstrated its specific distinctness by secondarily contacting the parental stock without interbreeding. The number of forms with the "potential" of developing into new species is unusually high, 0.8 per species in Australia, or 1.5 for Australia and New Guinea combined. The fundamental isolating barriers are tracts of arid country that cause extensive gaps in the habitats to which the various species are adapted. This presupposes an initial climatic deterioration which isolated remnant populations in "refuges", a theory that has already been introduced into ornithology by Gentili (1949), Mayr (1950), and Serventy (1951).

Climacteris differs from the related genus *Neositta* (nuthatches), studied by Mayr (1950), for in the latter a secondary climatic improvement has led to an increase in range and multiple hybridization. In *Climacteris* there is evidence of some secondary spread but, with one exception, distinctive geographically representative forms are still isolated.

I. INTRODUCTION

An unusual feature of several Australian bird genera is the occurrence of a large number of distinctive forms that replace each other geographically. Inevitably there is confusion as to the actual status of such forms for they can only be investigated by the study of large collections and adequate field work. Only after their limits have been determined can it be seen if they are separated by distributional barriers or, if they meet, whether they hybridize or behave as species to each other.

The present paper concerns the genus *Climacteris* Temminck (tree-creepers) a group that occupies a specialized "food niche", feeding on insects found on trunks and limbs of trees. They are to be seen characteristically hopping up and around trunks, securing insects from the cracks and fissures, a role for which the long, pointed bill and unusually strong legs and claws (see Plate 1) fit them well. The birds are about 6 in. in length and of somewhat drab colouring. There are six species in this genus.

Few Australian bird groups have been subjected to a modern speciation analysis. Cain (1955), in his study of the Australian platycercine parrots, has disclosed the existence of a number of differentiated isolated forms which have the "potential" of developing into new species. Of more relevance to the present study, because of closer phylogenetic relationship (Mayr and Amadon 1951), number of forms,

*Australian Museum, Sydney.

distribution, and habitat requirements is the recent work on the genus *Neositta* (nuthatches) (McGill 1948; Gentili 1949; Mayr 1950; Mack 1953). This genus has long been considered to be composed of six species in Australia and McGill (1948, Fig. 1) drew attention to the fact that these appeared to replace each other almost exactly. As such a situation would be contrary to current evolutionary theory, Mayr (1950) carried out a detailed taxonomic analysis and found that, despite significant morphological differences between the forms, several of them actually intergraded (hybridized) over a wide front, i.e. following prolonged isolation these forms had been approaching species status (judging from the extent of their morphological differences) but the distributional barriers broke down prematurely (before genetic distinctness had been reached). The result was multiple hybridization along contact fronts.

Distribution and speciation in many plant and animal groups in Australia is only comprehensible if it be postulated that the continent has been subjected to considerable climatic oscillations during and since the Pleistocene (cf. Crocker and Wood 1947). Of recent ornithologists, Mayr (1950) and Cain (1955) have accepted the theory that many geographically representative forms had their origin during an arid period (or periods) when remnant populations were isolated in a series of fertile pockets or "refuges" around the periphery of the continent. It will be shown in the present paper that such postulations are eminently suitable to explain distribution and speciation in *Climacteris*.

II. MATERIALS, METHODS, AND DEFINITIONS

The taxonomic section of this work was carried out on the bird collections of the American Museum of Natural History, New York (which includes the Mathews types), the Australian Museum, Sydney, National Museum, Melbourne, and Western Australian Museum, Perth. Mr. H. G. Condon has been good enough to check certain points on my behalf in the collections of the South Australian Museum, Adelaide.

Distributional and habitat data have been obtained from various sources, notably *The Emu*, Mathews (1923), and from other major works in ornithology. In addition, various aspects have been investigated by the author in the field, especially during the 1952 Australian Museum Expedition to central and northern Australia.

The study of geographic variation has followed standard taxonomic methods. For the sake of brevity measurements are given for *adult males* only. In most species, wing, tail, and bill measurements are tabulated but where it is obvious that neither tail length nor bill length vary geographically comparative measurements are given for the wing only. The wing, as has been shown by Amadon (1943), is a fairly good criterion of overall size in birds.

The following words require definition:

Isolate.—This is a population that is cut off from the main stock of the species by a distributional barrier. In the present work attention is directed only at isolates that have become differentiated. In that isolation is the first step in the speciation process these forms can be said to have the potential of developing into new species.

Habitat.—This term is used to mean the vegetation association in which a species lives. There is a remarkably close correlation between the major vegetation associations as defined by Prescott (1931) and the ranges of the different species of *Climac-*

TABLE 1
SPECIES AND SOME ISOLATES OF OLINACTERIS

Name	Dorsal Coloration	Ventral Coloration	Eyebrow	Wing Bar	Sexual Dimorphism	Habitat
Group 1 <i>C. erythropis</i>	Head sooty black, back deep (olive) brown, grey posteriorly	Fawn-grey only on upper breast in male. Abdomen heavily striated	Chestnut (also low eye)	Dull greyish buff	Moderate. Females only marked. Upper breast of female prominently marked with chestnut	Coastal sclerophyll, especially mountain forest (east)
<i>C. affinis</i>	Head deep grey, back mid brown	Fawn-grey, extends down over breast in male. Abdomen heavily striated	White (side of head flecked with white)	Rufous	Marked. Females as in <i>erythropis</i> but, in addition, has chestnut over white eyebrow	Mulga, also mallee (central areas)
Group 2 <i>C. picumnus picumnus</i>	Fairly uniform light grey-brown, head greyer	General colour fawn-grey. Striations finer and less marked	Fawn-grey and inconspicuous	Rich buff	Minor. Both sexes marked. Female with faint reddish markings on chest, male with faint blackish markings	Savannah and river forest (south-east)
<i>C. picumnus melanota</i>	Sooty black throughout. Pale tip of tail all but eliminated	As above, throat slightly paler, rest slightly darker	Whitish and pronounced	Pale to rich buff	Minor. Same as <i>p. picumnus</i>	Savannah (north-east)
<i>C. rufa rufa</i> *	Like <i>p. picumnus</i> but with slightly rufous tinge	Uniform rufous throughout (including throat). Striations lacking	Absent (whole side of head rufous)	Rufous	Minor. Same as <i>p. picumnus</i>	Sclerophyll and savannah (south-west)
<i>C. melanura melanura</i>	Sooty black above. No pale tip on tail	General colour chocolate-brown. No longitudinal striations	Absent (whole side of head black)	Off-white to buff	Marked. Female has white throat and chestnut and white striations on upper breast. In male, the chin, throat, and upper breast black streaked with white	Savannah (north-west and north)
<i>C. melanura vellei</i>	Like <i>m. melanura</i> but browner and duller	Like <i>m. melanura</i> but paler (rufous brown) ventrally	As for <i>m. melanura</i>	As for <i>m. melanura</i>	As for <i>m. melanura</i>	Savannah (mid-west)
Group 3 <i>C. leucophaea leucophaea</i> *	Deep grey-brown, grey posteriorly	Throat prominently white. Breast and abdomen greyish buff with longitudinal markings restricted to flanks	Absent (whole side of head dark)	Dull greyish buff	Moderate. Females only marked, having chestnut on side of head below eye. Immature females with reddish rump	Sclerophyll and rain-forest (east and south-east)
<i>C. leucophaea minor</i>	As for <i>l. leucophaea</i> but browner	As for <i>l. leucophaea</i> but much darker. White of throat practically eliminated. Ochraceous on abdomen	As for <i>l. leucophaea</i>	As for <i>l. leucophaea</i> (somewhat richer in colouring)	As for <i>l. leucophaea</i>	Rain-forest (north-east)
<i>C. leucophaea placens</i> <i>C. leucophaea steni</i> <i>C. leucophaea inaepectata</i> <i>C. leucophaea meridionalis</i>	These various New Guinea forms approach closely to <i>l. minor</i> . Like <i>l. minor</i> they are all small. They are briefly discussed under <i>leucophaea</i> in Section IV.					Mountain forests of New Guinea

*The forms *r. orientalis* and *l. griseescens* are not included as they barely differ from the nominate forms (see taxonomic section).

teris. Species are specialized for life in tropical rain-forest, sclerophyll forest, savannah (woodland and grassland), mulga, and mallee. In *Climacteris* the habitat occupied is almost as good a "species character" as structure and colour. Habitat is important in speciation because species restricted to discontinuous and "patchy" habitats frequently have morphologically differentiated isolates, whereas those inhabiting vegetation associations that are continuous do not.

III. THE SPECIES AND THEIR RELATIONSHIPS

The Checklist of the Royal Australasian Ornithologists Union (1926) credits *Climacteris* with nine species, as follows: *picumnus*, *rufa*, *melanota*, *leucophaea*, *minor*, *erythrops*, *affinis*, *melanura*, and *wellsi*. In their paper on the number of Australian bird species, however, Mayr and Serrenty (1944) list only seven species. Condon (1951) has advocated the more drastic course of recognizing only four.

On the basis of geographic replacement and similarity in colour pattern, three of the Checklist "species" can be reduced to race status, *minor* being nothing more than a distinctive race of *leucophaea*, *wellsi* of *melanura*, and *melanota* of *picumnus*. The New Guinea populations, generally grouped under the species *placens* (Mayr 1941) are no more different from typical *leucophaea* than is *minor* and should likewise be reduced to races of that species. Only in the case of *affinis* and *rufa* is there any cause for doubt as to status since Condon (1951) has placed them under *erythrops* and *picumnus* respectively and pointed out that they are geographical counterparts of those species. This course is not justified, however, especially with *affinis* which is an inhabitant of mulga and mallee, and the only species adapted to life under arid conditions. Its habitat is the antithesis of the mountain sclerophyll home of *erythrops*. The two, moreover, have distinctive characters, *affinis* differing in having acquired a white eyebrow marking, and a red "sex" mark on the side of the female's head. *C. rufa* is in every way the counterpart of *picumnus* in the south-west of the continent. It has reached a significant degree of differentiation (rufous colouring, absence of conspicuous striations from lower breast and abdomen) but remains isolated. Hence, from the evolutionary viewpoint it is impossible to say whether it is a form that is approaching, or has reached, species status. Taxonomic expediency, however, merits its being regarded as a species.

(a) Grouping of the Species

Climacteris falls into three species groups, with sex markings the best delimiting character. These are:

(i) *C. erythrops Group* (includes *affinis*).—The females have prominent chestnut markings on the upper breast but the male is unmarked. The female of *affinis* has an extra sex mark—a chestnut stripe over the "white" eyebrow of the species.

(ii) *C. picumnus Group* (*picumnus*, *rufa*, *melanura*).—There is a small sex marking in the centre of the upper breast in *picumnus* and *rufa*, black in males, reddish in females. In *melanura* the markings are enlarged, extending right to the chin, and the patterning is exaggerated.

(iii) *C. leucophaea Group*.—The female has a reddish sex mark on the side of the head and the male is unmarked.

Other characters confirm these subdivisions. Only *leucophaea* has a distinctive immature plumage, the rump (young females only?) being chestnut. The eggs are almost white and unlike those of other members of the genus (Campbell 1904) and the ventral striations are restricted to the flanks. The position of the sex marking (breast markings would tend to be obscured as the bird clings to dark trunks), occurrence of a "bright" rump in the young, and the white egg indicate that the *leucophaea* group has had a long independent development under conditions of dense forest. The *erythroptus* and *picumnus* groups are somewhat less distinctive. The former has acquired reddish markings on the side of the head and heavy ventral striations. The latter group of species is composed of relatively plain-coloured birds with reduced markings. They alone show a tendency towards ground feeding, a development associated with life in savannah woodland and grassland.

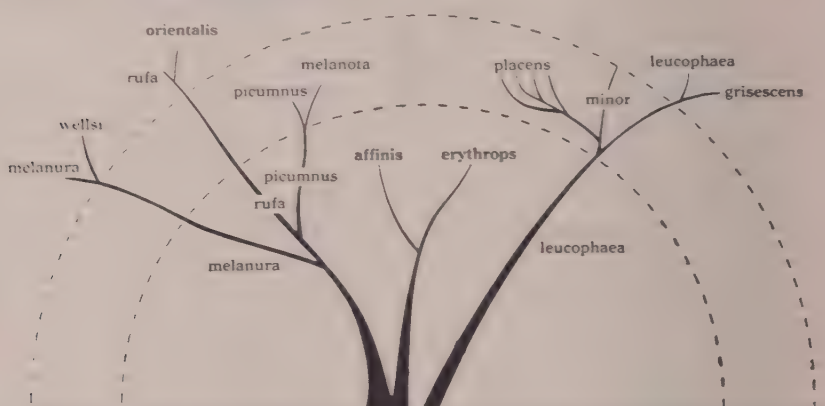


Fig. 1.—Suggested relationships of species and various isolates in *Climacteris*. Degree of divergence is given by distance from centre of base line. Those within the inner arc have reached species status, those between the inner and outer arc are well differentiated, and the outer limbs represent minor isolates.

The morphological characters of the species and major forms in the genus *Climacteris* are given in Table 1. Their relationships are set out in Figure 1.

IV. TAXONOMY

(a) *Intraspecific Variation*

CLIMACTERIS ERYTHROPTUS Gould

(red-browed tree-creeper)

Climacteris erythroptus Gould, 1841, Proc. Zool. Soc. Lond. 1840: 148.

Habitat.—Mountain and hill forests (coastal wet sclerophyll) of eastern Australia.

Geographic variation.—There is no significant colour variation in this species. Some Victorian birds have a darker head and back than is typical. Measurements of a series of adult males from different areas are set out in Table 2. There would appear to be no geographic variation in overall size in *erythroptus* but southernmost birds have longer bills. Thus *olinda* Mathews, 1916 (from Olinda, Vic.), wrongly

said to be distinguished by darker head and back, can be retained on these grounds. It presumably represents the end of a line in bill length. The measurements of the

TABLE 2
SIZE VARIATION IN *C. ERYTHROPS*

In this and subsequent tables the bill has been measured from the base of terminal feathers to the tip, the wing from its angle to the carpal, stretched along a rule, the tail from between the base of the central-most feathers to the tip. Mean values are shown in parenthesis in this table and in subsequent tables also

Locality	Sample Size	Bill Length (mm)	Wing Length (mm)	Tail Length (mm)
Adult males				
Emu Vale, Qld.	7	13.0-14.0 (13.6)	83-87 (86)	65-67 (66)
Tweed R., N.S.W.	1	13.6	86	64
Sydney area	10	13.5-14.2 (13.8)	85-91 (88)	61-66 (63)
Melbourne area	9	14.2-14.7 (14.3)	87-91 (89)	62-65 (64)
Adult females				
Sydney area	8	13.2-14.0 (13.6)	82-86 (84)	56-62 (59)

females from the Sydney area (Table 2) show that there is a slight difference in size between the sexes. This is typical also of other members of the genus.



Fig. 2.—Range of *Climacteris erythroptera* (1) in the coastal mountain sclerophyll forest of the east, and of *C. affinis* (2), an inhabitant of the mallee and desert mulga regions of the continent.

Specimens seen. QUEENSLAND: Emu Vale (1). NEW SOUTH WALES: Tweed R. (2). DISTRICT: 40; Blue Mountains (18). VICTORIA: Melbourne area (16). Numerous at various representative sites of sample of adult birds.

Distribution. Blue Mountains, N.S.W., to Gisborne, Vic. (skin from latter locality in National Museum Collection). Its range is shown in Figure 2.

CLIMACTERIS AFFINIS Blyth

(white-browed tree-creeper)

Climacteris affinis Blyth, 1864, J. Asiat. Soc. Beng. 32: 453.

Habitat.—Mulga and mallee areas of dry central regions of the continent. This is the desert representative of the genus. In contrast to *picumnus* it is found far away from watercourses (Marshall 1933).

Geographic variation.—Variation in this species is minor. The author cannot distinguish between birds from New South Wales, central Australia, and the west coast of Australia. Howe (1921) credits mallee birds from the south with being larger and paler (whiter) than the typical. Condon (1951) has commented upon this and subsequently informed the author that "southern birds seem to differ slightly in being more distinctly streaked below". The distinction would appear to be minor, however, and the few specimens from South Australia seen by the author fail to support the race *parsoni* Mellor, 1919 (Mathews 1923). The race *neositta* Mathews, 1912, described from Callion, mid-western Australia (Mathews 1923), is certainly not warranted.

TABLE 3

SIZE VARIATION OF ADULT MALES OF *C. AFFINIS*

Measurements of South Australian birds are by Mr. H. G. Condon (personal communication)

Locality	Sample Size	Wing Length (mm)	Tail Length (mm)
Bulloo, Qld.	1	89	57
Western New South Wales	7	86-94 (89)	53-57 (54)
South Australia	9	87-94 (89)	50-57 (54)
Central Australia	10	87-91 (89)	52-57 (55)
Mid-western Australia	8	86-91 (89)	51-60 (56)
South-western Australia (Kalgoorlie-Naretha area)	3	88-91 (89)	53-59 (55)

The measurements of samples from different parts of the range are set out in Table 3. There is no geographic size variation in *affinis*. Mallee birds are not larger as stated by Howe (1921). In males the bill length ranges from 11.5-12.3 mm, without geographic variation. This is decidedly smaller than in *erythrops* (see Table 2).

Specimens seen.—QUEENSLAND: Bulloo (1); Tibooburra (2). NEW SOUTH WALES: Moolah, Clare, Broken Hill, Belmore, near Wentworth (11). SOUTH AUSTRALIA: McDonald Park, Lake Gardner, Nanning, Kallioota, Paringa, Taplan, Murtho, Pungonda (12). CENTRAL AUSTRALIA: Todmorgen, Morillana, Finke R., MacDonnell Ranges (15); WESTERN AUSTRALIA: Manilya, East Murchison, Yalgoo (12); Kalgoorlie and Naretha (6).

Distribution.—The range limits appear to be Collarenebri, N.S.W., in the east (J. Lawson, personal communication), and the Victorian Mallee, Gawler Ranges, S.A. (Terrill and Rix 1950), Nullarbor Plain, Kalgoorlie, and Southern Cross, W.A. (Serventy and Whittell 1951) in the south. The northern limits are apparently along the line joining Carnarvon, W.A., Alice Springs, N.T. (Whitlock 1924), and Charleville, Qld. (Marshall 1933). Thus *affinis* has a continuous distribution but its occurrence is scattered (Terrill and Rix 1950). Its range is shown in Figure 2.

CLIMACTERIS PICUMNUS Temminck & Laugier

(brown tree-creeper)

Climacteris picumnus Temminck and Laugier, 1824, Planch. Color. Ois. (livre 47) 3: 281.

Habitat.—Savannah woodland and grassland, extending back into arid country where there are eucalypts along streams (e.g. rivers entering the eastern side of Lake Eyre basin).

Geographic variation.—There are two distinct colour races of *C. picumnus*—*C. picumnus picumnus* in the south-east of Australia, and *C. picumnus melanota* in northern Queensland (Cape York).

C. p. picumnus does not vary significantly in colour throughout its range. The author agrees with Condon (1951) that the Victorian and South Australian birds should not be recognized as races, so that *victoriae* Mathews, 1912 and *australis* Mathews, 1912 (Mathews 1923) are placed in synonymy. Condon (1951), with reference to the race *waitei* White, 1917 (from Innamincka, Qld.) stated that a pair of birds from Cooper's Creek, Qld., are characterized by their whitish throats and less prominent ventral stripes. In a letter to the author he wrote that "the type specimen and a female collected at the same time (he does not regard the type as a juvenile) are in a bedraggled condition but would appear to be less strongly marked below than typical southern *p. picumnus*. They can, however, be matched with one or two other skins from the south." In the Australian Museum collection there are two worn birds from Rockhampton, Qld., that approximate to those described from Cooper's Creek. They are paler, generally, so that the eyebrow marking is whitish, as is the throat, the wing bar is lighter in colour, and the grey of the breast is much reduced. Thus geographic colour variation in *p. picumnus* is of a minor clinal nature, insufficient to warrant the recognition of additional races.

The black tree-creeper of Cape York is, as noted, only a distinctive colour race of *picumnus* and is correctly named *p. melanota*. Specimens of this form from Barron R., Walsh R., and Normanton, Qld., are similar in coloration. A single male and female from the Watson R., Cape York, are darker ventrally and equal to the darkest of the others in dorsal coloration. This suggests that there is a northward cline of increasing pigmentation in the Cape York race.

C. p. melanota obviously arose in isolation and it is important to know whether or not it is still isolated or is now connected with the southern form by a hybrid zone. However, no intermediates between *p. picumnus* and *p. melanota* have been seen. Birds from Cardwell, Qld., at the southern (known) range limit of the latter, are described as being "fuscous" instead of "fuscous-black" above and to show an obscure tail band (Barnard 1926). The author has seen this material and confirms that these birds are paler (brownier) dorsally than the more northern material and hence do tend somewhat towards *p. picumnus*.

Measurements of samples of adult males from different parts of the range are set out in Tables 4 and 5. Wing length measurements, a criterion of overall size in birds (Amadon 1943), indicate that there is no significant geographic variation in *p. picumnus*. Material of *p. melanota* is insufficient to decide the status of the form *barroni* Mathews, 1915 (from Cairns, Qld.), said to be larger in size and greyer on

the under surface than the nominate form from Lynd R., Qld. Three males from Normanton, however, are smaller than those to the east (Table 4), and a size cline could be involved. It is difficult to deal with the minor variation in *p. melanota* nomenclatorially, and the only satisfactory course is not to subdivide it.

TABLE 4
SIZE VARIATION IN WING LENGTHS OF ADULT MALES OF TWO FORMS OF *C. PICUMNUS*

<i>C. p. picumnus</i>			<i>C. p. melanota</i>		
Locality	Sample Size	Wing Length (mm)	Locality	Sample Size	Wing Length (mm)
Adelaide area	6	92-100 (96)	Kirrama Tableland		
Victorian Mallee	5	89-96 (93)	near Cardwell, Qld.	4	92-97 (94)
Melbourne area	5	90-95 (93)	Barron R., Qld.	3	93-99 (96)
Sydney area	8	95-99 (97)	Walsh R., Qld.	2	91 and 97
Bourke and Darling R., N.S.W.	4	92-95 (94)	Normanton, Qld.	3	87-91 (89)
Ipswich, Qld.	1	93	Watson R., Cape York	2	92 and 97
Rockhampton, Qld.	1	89	Coen, Cape York	2	91 and 94

Wing, bill, and tail-length measurements of male specimens of *p. picumnus* and *p. melanota* (see Table 4) have been averaged in Table 5. It will be seen that *p. picumnus* is larger in all measurements.

TABLE 5
MEAN SIZE VARIATION OF ADULT MALES OF TWO FORMS OF *C. PICUMNUS*

Form	Sample Size	Wing Length (mm)	Bill Length (mm)	Tail Length (mm)
<i>C. p. picumnus</i>	30	89-100 (95)	12.9-14.0 (13.4)	59-70 (64)
<i>C. p. melanota</i>	16	87-99 (93)	12.5-13.8 (13.1)	57-68 (61)

Specimens seen

C. p. picumnus.—SOUTH AUSTRALIA: Adelaide area (9). VICTORIA: Melbourne area (9), Mallee area (8). NEW SOUTH WALES: Bourke, Brewarrina, Wilcannia, Darling R. (8), odd specimens from various localities in near-land region, Sydney area (12), Richmond R. (5). QUEENSLAND: Cooper's Creek (2), Innesmore, Ward R., near Charleville (2), Ipswich (1), Duaringa, near Rockhampton (2).

C. p. melanota.—QUEENSLAND: Normanton (5), Walsh R., west of Cairns (4), Barron R. (5), Kirrama Tableland, near Cardwell (5), Watson R. (2), Coen area (3).

Distribution

C. p. picumnus.—Longitude 136° E., near Adelaide (Terrell and Rix 1950) eastwards to the outskirts of Melbourne and Spicers, and north to the river entering the eastern side of Lake Eyre, Charleville, and Rockhampton (Fig. 3, I).

(ii) *C. p. melanota*.—From Cape York south to the Kurrumba Tableland near Cardwell and west to the upper Flinders R. (Berney 1905) and Normanton (Fig. 3, 1a).

No information is available as to the occurrence of *p. pictus* between Rockhampton and Cardwell but as the area is covered by savannah woodland it can be anticipated that the two forms approach closer to each other than these two points. It might be noted that there is an old sight record of *p. pictus* from the Suttor R., a branch of the Burdekin R., by Gilbert (Chisholm 1945).

CLIMACTERIS RUF A Gould

(rufous tree-creeper)

Climacteris rufa Gould, 1841, Proc. Zool. Soc. Lond. 1840: 149.

Habitat.—Sclerophyll forest (jarrah belt), savannah woodland, and extending out into the semi-arid "big mallee" country of Whitlock (Mathews 1923), in the south-

TABLE 6
SIZE VARIATION OF ADULT MALES OF *C. RUF A*

Locality	Sample Size	Wing Length (mm)	Tail Length (mm)
South-western Australia	17	87-94 (91)	59-68 (63)
Gawler Ranges, S.A.	10	92-98 (95)	63-70 (66)

west corner of the continent, and occupying savannah woodland on Eyre Peninsula. The remarks of Serventy and Whittell (1951) as to the relatively great habitat tolerance of this species should be noted a feature, as they pointed out, of a number of south-western species and races.

Geographic variation.—Colour variation is minor, birds from the lower rainfall areas (Woolundra, Kalgoorlie, Gawler Ranges) being paler than others. The south-west coastal and inland populations have been separated racially, the grounds being these slight colour differences plus the alleged longer bill and shorter wing of the former (*obscura* Carter, 1910 (Mathews 1923)). Actually there is no difference in measurements and the author supports the view of Condon (1951) that this race should be reduced to synonymy as the colour differences alone are inadequate. The birds from South Australia have been named *orientalis* Mathews, 1912, and are said to be "paler above and below". Condon (1951) credits this form with having the male fore neck marking slightly more prominent, which seems correct.

The measurements of samples of adult males of *rufa* from Western Australia and South Australia are set out in Table 6. The larger measurements of the eastern birds confirm *orientalis* as a race.

Specimens seen.—WESTERN AUSTRALIA: Lake Muir, Warren R., Mt. Barker, Wilson's Inlet, Vasse, Woolundra, Kalgoorlie, Katanning, Wongan Hills, Beecroft Hill, Ongerup, Mongup, Albany, King George Sound (40). SOUTH AUSTRALIA: Gawler Ranges, Donald's Pinn., Corbidge, Nonning, 25 miles S. of Iron Knob, Wilcherry (16).

Distribution.—South of the mulga-eucalypt line in Western Australia (Serventy and Whittell 1951) with the most easterly records of Whitlock being points 100 miles east of Geraldton, and at Zanthus, 130 miles east of Kalgoorlie (Mathews 1923). There is a gap of some 600 miles in the region of the Nullarbor Plain. In South Australia the species is restricted to the general region of the Gawler Ranges (Terrill and Rix 1950). Its distribution is shown in Figure 3 (3 and 3a).

CLIMACTERIS MELANURA Gould
(black-tailed tree-creeper, Plate 1)

Climacteris melanura Gould, 1843, Proc. Zool. Soc. Lond. 1843: 138.

Habitat.—Savannah woodland and savannah grassland of the mid west and north of the continent.



Fig. 3.—Distribution of species and distinctive isolates (indicated by numbers) in the *Climacteris picumnus* group. Black arrows and capital letters refer to isolating barriers. Clear arrows on outside of map indicate secondary range extensions. 1, *C. p. picumnus*; 1a, *C. p. melanota*; 2, *C. m. melanura*; 2a, *C. m. wellsi*; 3, *C. r. rufa*; 3a, *C. r. orientalis*.

Geographic variation.—The population isolated in the Gascoyne R.—De Grey R. area of the mid west (*m. wellsi* Ogilvie-Grant, 1909) differs from *m. melanura* in that the ventral surface is deep rufous-brown instead of black and dark brown, and the under-tail coverts are prominently barred (Fig. 4; see also plate in Campbell 1923). Elsewhere there is a tendency for birds from drier areas to be paler. Specimens from Alexandria are examples of this (*m. alexandrae* Mathews, 1912), Mathews (1923) describing this form as being “much paler below”. Howe (1921) has drawn attention to the tendency for its under-tail coverts to be barred instead of uniformly dark. Thus it shows trends culminating in the distinctive *m. wellsi*. The differences are, however, sufficiently great to warrant *m. alexandrae* being retained as a race.

Insufficient material is available to adequately consider geographic size variation. Bill lengths of adult males range from 13.4–14.0 mm, and tail lengths from

66–73 mm, apparently without geographic variation. Wing-length measurements are set out in Table 7.

Specimens seen

(i) *C. m. melanura*.—WESTERN AUSTRALIA: Derby (12), junction of the Fitzroy and Margaret Rs. (1), Napier, Broome Bay (4). NORTHERN TERRITORY: Pine Creek (4), Alexandria (3). QUEENSLAND: Mt. Isa (1), Gregory R. (3).

(ii) *C. m. wellsi*.—WESTERN AUSTRALIA: Strelley R. (5).

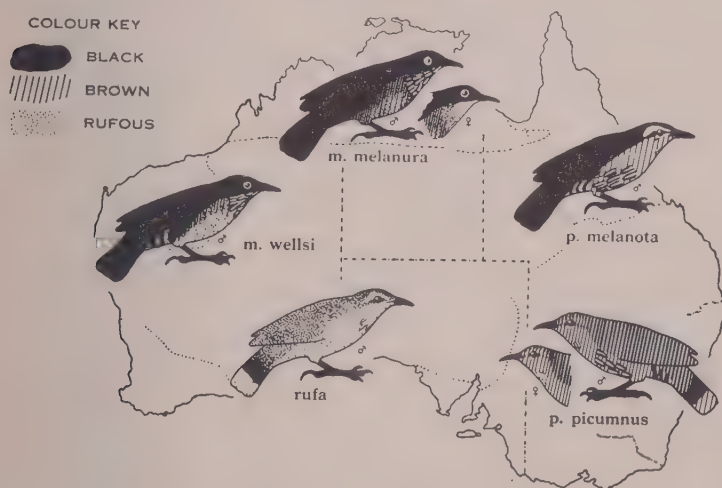


Fig. 4.—Species and major isolates of the *Climacteris picumnus* group to show morphological characters. *C. r. orientalis* is not shown as it differs from the nominate form in only minor ways (B. Bertram del.).

Distribution

(i) *C. m. melanura*.—Fitzroy R. in the north-west and northwards and eastwards to the Gregory, Leichhardt, and Cloncurry Rs. (MacGillivray 1914, 1929; Keast, field observations July 1952) where it is common (Fig. 3, 2). Most easterly records are from the Lynd R., Qld. (Chisholm

TABLE 7
SIZE VARIATION IN WING LENGTHS OF ADULT MALES OF *C. MELANURA*

Locality	Sample Size	Wing Length (mm)
Derby, W.A.	8	95–102 (98)
Napier–Broome Bay, W.A.	2	Each 100
Pine Creek, N.T.	3	96–99 (97)
Alexandria, N.T.	2	Each 97
Gregory R., Qld.	2	97 and 99

1945) and Einasleigh, Qld. (Keast, field observations July 1952), within the range of *C. picumnus melanota*. The most southern record of *C. m. melanura* in the Northern Territory is that from Bunka Banka, south of Newcastle Waters (Jarman 1944).

(ii) *C. m. wellsi*.—Gascoyne R. to De Grey R., W. A. (Fig. 3, 2a).

CLIMACTERIS LEUCOPHAEA (Latham)

(white-throated tree-creeper)

Climacteris leucophaea (Latham), 1801, Ind. Orn. Suppl. 1801: 36.

Habitat. Sclerophyll and rain-forests in eastern Australia, extending inland where there are dense riverside savannahs. In New Guinea the species occupies mountain forests.



Fig. 5. Distribution and speciation in *Climacteris leucophaea*. The morphologically differentiated isolates are numbered 1-7. Distributional barriers within Australia are indicated by arrows and the letters E and F. 1, *C. l. leucophaea*; 2, *C. l. griseescens*; 3, *C. l. minor*; 4, *C. l. placens*; 5, *C. l. steini*; 6, *C. l. inexpectata*; 7, *C. l. meridionalis*.

Geographic variation.—Mainland stocks may be divided into the following groups:

(i) Central Queensland to western Victoria and south-eastern South Australia (*C. l. leucophaea*, Fig. 5, 1). The Bunya Mountains specimens are slightly darker dorsally and somewhat richer in tone ventrally than those from the Sydney area. Specimens from the Melbourne area, by contrast, would appear to be slightly paler ventrally and darker dorsally. The variation is minor and clinal.

(ii) Mount Lofty Ranges, S. A. (*C. l. griseescens* Mathews, 1912, Fig. 5, 2). This form is the palest ventrally, being almost white. Some Victorian birds (e.g. one from Olinda, near Melbourne) could fit here with respect to colour but not size—Table 8.

(iii) Rain-forests of the Atherton area, north-eastern Queensland (*L. minor* Ramsay, 1891, Fig. 5, 3). This is a small, very dark race. The chest is grey-brown instead of white or buff-white, and the throat is grey instead of white. The abdomen and under-tail coverts are dark ochraceous and heavily flecked throughout with blackish brown, whereas in *L. leucophaea* the central part of the ventral surface lacks the spotting. Dorsally, the birds are much like those from the south but, if anything, are slightly more richly coloured.

Size variation in *leucophaea* will be seen from samples of adult males from different parts of the range set out in Table 8. These measurements confirm the distinctness of the populations isolated in the Mount Lofty Ranges and rain-forests of the Cairns-Atherton area.

Four forms are recognized from New Guinea under "*Climacteris placens*" (Mayr 1941). All of these are, in fact, less different from *L. minor* (Cairns area) than the latter is from *L. leucophaea*, hence they must be included under that species. The chief

TABLE 8
SIZE VARIATION OF ADULT MALES OF *C. LEUCOPHAEA*

Locality	Sample Size	Bill Length (mm)	Wing Length (mm)	Tail Length (mm)
Mount Lofty Ranges, S.A.	4	14.8-15.8 (15.4)	94-97 (95)	62-64 (63)
Orway Ranges, Vic.	4	14.7-15.0 (14.8)	88-95 (92)	58-62 (60)
Melbourne	10	13.8-14.4 (14.0)	88-92 (80)	59-63 (60)
Sydney	10	13.6-14.1 (13.9)	86-92 (89)	56-63 (60)
Emu Vale, Qld.	8	13.2-14.0 (13.8)	86-97 (91)	59-66 (62)
Cairns-Atherton area, Qld.	12	12.0-12.8 (12.4)	78-85 (82)	52-60 (56)

innovation of the New Guinea stocks is the development of spotting on the forehead, a character only vaguely discernible in *L. minor*. The four forms would appear to be completely isolated in mountain ranges in different parts of New Guinea (Fig. 5, 4-7).

It is not proposed to treat the New Guinea forms beyond noting the main characters. The ranges are from Mayr (1941).

(1) *L. placens* Schater, 1874 (Mountains of Vogelkop). The top of the head lacks the pale spotting but is suffused with dark chestnut. The ventral surface is a shade darker than that of Cairns birds. Specimens from Arfak.

(2) *L. steini* Mayr, 1936 (Weyland Mountains). There is pale spotting through a sooty black crown. The ventral surface is dark ochraceous brown. Specimens from Mt. Taffa.

(3) *L. inexpectata* Rand, 1940 (northern slopes of Oranje Mountains). This form is distinctly paler below, the throat being white and the breast grey. Specimens from Lake Habbema.

(4) *L. meridionalis* Hartert, 1907 (mountains of south-east New Guinea and Herzog Mountains). This is like *L. placens* but has pale crown fleckings and slightly more ochraceous ventral surface. Specimens from the Mambare R.

Measurements of nine adult males range from 84–90 mm for the wing length, the two largest specimens belonging to *l. inexpectata*, 10·8–12·0 mm for bill length, and 59–70 mm for the tail, with *l. inexpectata* again tending to be the largest. From these measurements and Table 8 it would appear that the New Guinea birds have shorter bills and slightly longer wings and tails than the Australian *l. minor*.

Specimens seen.—SOUTH AUSTRALIA: Mount Lofty Ranges (7). VICTORIA: Western Victoria (2), Otway Ranges (6), Melbourne area (15). NEW SOUTH WALES: Riverina (2), Bourke (2), Blue Mountains (5), Sydney area (20), Port Stephens (2), Bellingen R. (5), Tweed R. (2). QUEENSLAND: Emu Vale (6), various localities in the Atherton area (18). Specimens of the various New Guinea races were also seen.

Distribution.—Mount Lofty Ranges, S.A., to Rockhampton, Qld. (Barnard and Barnard 1925; Wolstenholme 1925), occurring sparingly in Tasmania (Sharland 1945), and with a dense concentration in the rain-forests of the Atherton area of north Queensland. Whilst distribution is essentially coastal, *leucophaea* extends well inland where there are dense riverside forests (skins from the Riverina, Watercourse near Moree, and Bourke, N.S.W.). The distribution is set out in Figure 5.

Thus *C. leucophaea* has several isolates. *C. l. grisescens*, from the Mount Lofty Ranges, is cut off from the main stock by the 50–100-mile-wide tract of arid country in the south-east of South Australia (Coorong area). *C. l. minor* of the Cairns–Atherton area, inhabiting rain-forest instead of sclerophyll forest, is likewise isolated by a tract of arid country. This barrier extends southwards from Mt. Spec, near Townsville, and is at least 100 miles wide. Torres Strait, a water barrier, separates the New Guinea forms from Australia. These in turn, inhabiting different mountain ranges, would appear to be isolated from each other.

(b) Nomenclature and New Synonymy

Climacteris erythroptus erythroptus Gould, 1841.

Climacteris erythroptus olinda Mathews, 1916.

Climacteris affinis Blyth, 1864. Synonyms: *parsoni*, *neositta*.

Climacteris picumnus picumnus Temminck & Laugier, 1824. Synonym: *waitei*.

Previously reduced to synonymy; *victoriae*, *australis*.

Climacteris picumnus melanota Gould, 1846. Synonym: *barroni*.

Climacteris rufa rufa Gould, 1841. Previously reduced to synonymy: *obscura*.

Climacteris rufa orientalis Mathews, 1912.

Climacteris melanura melanura Gould, 1843.

Climacteris melanura wellsi Ogilvie-Grant, 1909. Previously reduced to synonymy: *striata*.

Climacteris melanura alexandrae Mathews, 1912.

Climacteris leucophaea leucophaea (Latham), 1801.

Climacteris leucophaea grisescens Mathews, 1912.

Climacteris leucophaea minor Ramsay, 1891. Previously reduced to synonymy: *northi*.

V. SPECIES FORMATION

Speciation is now generally accepted as occurring by the following steps:

- (i) Part of the population of a species becomes isolated, geographic barriers prohibiting reproductive contact with parental stock.

- (ii) Under conditions of isolation, morphological, ecological, and genetic differences start to develop.
- (iii) These differences become increasingly great.
- (iv) In the ideal case, the isolated forms eventually come together again. If specific distinctness has been attained they do not interbreed, but if not a hybrid zone is formed.

At any time differentiating isolates may be re-united as they have only the "potential" of developing into new species. Once this happens the speciation process comes to a halt. At the other extreme, the diverging stocks may remain isolated indefinitely. Eventually a stage is reached where they are less like the parental stock than are other known species in the genus. At this point it is justifiable to make an arbitrary decision and, for taxonomic purposes, regard them as species. This can never be a completely satisfactory method for many cases of sibling species are known in which the two are barely distinguishable on morphological grounds.

(a) *Forms with the Potential of Developing into New Species*

Speciation is actively occurring in *Climacteris* and all stages in the process can be recognized. Thus there are two isolates within Australia (*C. grisescens*, *C. orientalis*) starting to differentiate, one isolate (*C. wellsi*) that is moderately well differentiated, and two (*C. minor*, *C. melanota*) that are well differentiated. One form (*C. rufa*) is so distinctive that, notwithstanding complete isolation, it can reasonably be regarded as a species.

One form (*C. melanota*) has resumed contact with *C. melanura* and, by failing to interbreed, has demonstrated that it has reached specific distinctness. No forms have as yet resumed contact prematurely—which would be shown by the occurrence of a hybrid zone.

The ranges of the various isolates in *Climacteris* and the locations of the distributional barriers can be seen in Figures 3 and 5. The degree of differentiation attained by the major isolates in the *picumnus* group (*C. rufa*, *C. melanota*, *C. wellsi*) will be seen from Figure 4.

Thus the genus *Climacteris* has five morphologically differentiated isolates in Australia (excluding *C. rufa*) in the six species. It could thus be said to have 0.8 forms per species with the potential of developing into new species. There are another four isolates in New Guinea so that the figure for the genus as a whole is 1.50.

(b) *Distribution and Habitat*

The distribution of the various species and major geographic forms (Table 1) is plotted on Figures 2-5. Two points may be noted at the outset. Firstly, there is virtually no part of the continent from which the genus is absent, and secondly, the coexistence of more than one species in an area is more apparent than real, for different habitats are occupied. It so happens in *Climacteris* that where two species occupy adjacent habitats in an area they are members of different species groups. These distributional relationships fall into the following two categories:

(i) *Species Occupying Adjacent Habitats and the Origin and Maintenance of Habitat Differences.*—The habitats of the species and major forms of *Climacteris* are

set out in the last column of Table 1. Members of the *picumnus* group are inhabitants of savannah woodland and grassland (with *rufa* also inhabiting sclerophyll forest). *C. leucophaea* inhabits sclerophyll forest in the south-east and rain-forest in the north-east of the continent. In the *erythrops* species group there is a peculiar dichotomy, the nominate species occupying mountain sclerophyll where the rainfall is high and *affinis* desert mulga and mallee.

The way in which habitat differences serve to keep species of *Climacteris* apart can be seen in south-eastern Australia. Here the major forest associations are arranged into zones. There is a north-south strip of sclerophyll between the Great Dividing Range and the coast and it is here that *leucophaea* occurs (Fig. 5). In the higher mountain forests, a part of this, *erythrops* is concentrated (Fig. 2). *C. picumnus*, by contrast, keeps to the savannah woodland that is distributed over the western slopes of the mountains and extends from there inland. (Fig 3, 1). Each species keeps strictly to its habitat, occurring wherever the habitat does. Thus, where there is a belt of savannah seaward of the Dividing Range, *picumnus* is to be found and *leucophaea* occurs inland where there are dense riverside forests approximating in density to coastal sclerophyll. In a few places (e.g. Capertee Valley, N.S.W.) where the habitats merge, all three species are present.

An interesting ecological problem is the determination of the factors which restrict a species to a particular habitat. In the case of *leucophaea* and *picumnus* there would appear to be no doubt that density of the trees is all important. The former is exclusively an arboreal feeder, whilst the latter obtains much of its food from the ground. "Sclerophyll" and "savannah" are essentially terms for "high tree density with undergrowth" and "low tree density with open ground" respectively. No ready reason can be seen for the restriction of *erythrops* to mountain forests.

Since habitat is almost as good a "species character" as morphology in *Climacteris* the problem presents itself as to how members of a genus become specialized to life in different habitats. Unfortunately the present study does not provide an answer to this. Two cases of geographic variation in the habitat occupied by a species need comment. Firstly, the northern isolate of *leucophaea* (*minor*) inhabits rain-forest, not sclerophyll. Accordingly, it could be said to have developed habitat differences along with the morphological ones. If, as a result of climatic and vegetational changes, these forms resume contact it is a reasonable supposition that one will be at an advantage in or "prefer" sclerophyll forest and the other rain-forest. It follows that if, during isolation, specific distinctness had been reached, they could come to live side by side, each keeping to its own habitat. Secondly, in the south-west of the continent *r. rufa* inhabits sclerophyll, savannah, and "big mallee", but its outlier on Eyre Peninsula, 800-900 miles to the east (*r. orientalis*), is restricted to savannah, which is the only habitat available. A climatic deterioration is likely to have a much greater adaptational effect on the latter, since it is already isolated in a relatively dry area, than on the main stocks in the mountainous and well-watered south-west. It will be faced with the alternative of adapting itself to conditions of semi-aridity or of becoming extinct. If the vagaries of climate subsequently re-unite the two stocks it is a reasonable supposition that *r. orientalis* will be at an advantage under dry conditions over the less adapted *r. rufa*. There may then be a duplication of the position in the south-east where sclerophyll and savannah are occupied by different species.

It is difficult to see how the desert *affinis* could have been derived from the sclerophyll *erythrops* (or vice versa) other than by some such succession of circumstances as that postulated here.

(ii) *Species and Forms Occupying Equivalent Habitats in Different Parts of the Continent*.—The bulk of these occur in the *picumnus* group. Between them they occupy the whole of the savannah woodland areas of the continent, as will be seen from Figures 3 and 4. Clockwise around the continent, and isolated by a series of distributional barriers, these species and forms are: *p. picumnus*, *r. orientalis*, *r. rufa*, *m. wellsi*, *m. melanura*, and *p. melanota*. *C. leucophaea* has a series of forms stretching from New Guinea down the east coast of Australia to the Mount Lofty Ranges in South Australia (Fig. 5), occupying forests of the dense rain-forest and sclerophyll type.

The geographically representative species and forms in these species groups represent relicts of former continuously ranging stocks. They are the forms that have the potential for developing into new species and their existence is due to the secondary development of isolating barriers.

(c) Isolating Barriers

The major distributional barriers and the forms isolated by them are given below. Their geographic position is indicated by arrows on Figures 3 and 5.

(i) Spencer Gulf and the arid country about its head (Fig. 3, *A*: separating *p. picumnus* from *r. orientalis*). Although quite narrow (50–100 miles) this is of fundamental importance, representing the eastern range limit of several south-western species and races.

(ii) Nullarbor Plain (Fig. 3, *B*: separating *r. orientalis* from *r. rufa*). There can be little doubt that the species *r. rufa* arose to the west of this barrier and, with a minor climatic improvement, was able to extend across it to the east. Separation of the Eyre Peninsula form would appear to be relatively recent.

(iii) Arid tract in the region of Geraldton–Shark Bay, W.A. (Fig. 3, *C*: separating *r. rufa* from *m. wellsi*). This is a major distributional barrier in Australian birds. It divides the most southern elements of the Kimberley avifauna from the south-western one.

(iv) Arid tract extending from the Great Sandy Desert to the sea in the region of Ninety Mile Beach (Fig. 3, *D*: separating *m. wellsi* from *m. melanura*). This barrier isolates the Kimberley avifauna proper from its numerically impoverished derivative in the Gascoyne R.–De Grey R. section of the continent.

(v) Dry barrier in north-eastern Queensland (Fig. 5, *E*: separating *l. minor* from *l. leucophaea*; Fig. 3, *E*: separating *p. melanota* from *p. picumnus*). This barrier cannot be clearly seen so far as *picumnus* is concerned (since it is a savannah species) but is presumably the tract of dry country that reaches the coast in the Townsville–Inkerman area. The corridor must formerly have been drier. Apart from *picumnus* other savannah bird species have distinct forms to the north and south of it, notably *Seisura inquieta* and *Poephila cincta*. As the vegetation map of Prescott (1931) shows savannah to extend continuously from north to south there could at the present time be secondary contact of the forms in these species.

(vi) Ninety Mile Desert in south-eastern South Australia which separates the sclerophyll forests of the Mount Lofty Ranges from those of western Victoria (Fig. 5, *F*: separating *l. leucophaea* and *l. griseocens*). This is a minor barrier but several sclerophyll-inhabiting birds have a distinct race to the west of it.

It will be noted that all the distributional barriers postulated are, in effect, dry sections from which the particular habitat of a species is absent. A former barrier, not shown on Figure 3, must have been the dry country extending from inland to the head of the Gulf of Carpentaria. There can be no doubt that *melanura* developed in the north-west of the continent became adapted to somewhat dry conditions there, as did various other north-western species (Keast 1956), and has since spread eastwards to meet *p. melanota* on the eastern side of the Gulf.

TABLE 9
CONTINENTAL DISTRIBUTION OF SPECIES AND ISOLATES OF CLIMACTERIS COMPARED WITH TWO OTHER GENERA

Section of Continent	<i>Climacteris</i> (3 species groups)	<i>Neositta</i> (1 species group)	<i>Platycercus</i> (2 species groups)
North-western section	1 species	1 very distinct race	1 species
Cape York	1 very distinct race	1 very distinct race	1 minor form
Atherton area	1 very distinct race	1 minor race	1 distinct race, 1 minor race
South-eastern section	2 species	1 very distinct race	2 species
South-western section	1 species	1 very distinct race	1 species
Murray basin	1 species	—	1 species
Mount Lofty Ranges	1 minor race	—	1 distinct race
Eyre Peninsula	1 minor race	—	—
Hamersley area (mid-west)	1 distinct race	—	—

(d) *Climacteris* and the Refuge Theory

It is apparent that speciation and distribution in *Climacteris* can only be interpreted in terms of past climatic and vegetational changes. There is now abundant geological evidence (Browne 1945) that during and since the Pleistocene the Australian continent has been subjected to climatic cycles, at the height of which it has been both less and more arid than today. During fluviatile periods it is obvious that plants and animals requiring a high to moderate rainfall must have been widely distributed. An increase in aridity would have initiated an extension of the central desert towards the periphery of the continent and tongues of dry country that contemporaneously extend through to the sea (Nullarbor Plain, Ninety Mile Beach in north-western Australia, etc.) would have been even more formidable barriers than they are today. Distributions must have contracted and been broken up, species requiring medium to high rainfall only being able to persist in peripheral refuges where they were insulated against the full effects of the climate.

It is significant that, with the exception of the desert species *affinis*, the various species and distinctive forms of *Climacteris* are "centred" in hilly or mountainous areas or others that, because of the configuration of the country, receive a moderate

to high rainfall. Thus, *leucophaea* (requiring sclerophyll and rain-forests) has a form isolated in the Atherton Mountains, another in the Great Dividing Range of south-eastern Australia, and a third in the Mount Lofty Ranges in South Australia. Within the *picumnus* group (savannah forms), *melanura* has obviously radiated out from the mountainous and good rainfall region in the north-west (Kimberleys and Arnhem Land), as has *p. melanota* in the north-east, *p. picumnus* in the south-east, and *rufa* in the south-west. There is no doubt that these various species and forms developed exactly where they occur today, isolated in sections of the continent that were least affected by the encroaching aridity, and that they have secondarily spread from there.

Comparison with the findings of Mayr (1950) in *Neositta* and Cain (1955) with *Platycercus* indicates that there is marked correspondence in the areas where the species and distinctive forms arose in the three groups. This will be seen from Table 9. This tabulation is exhaustive only for *Climacteris*. In both *Neositta* and *Platycercus* there is a chain of forms down the Queensland coast. A species of *Platycercus* has developed in Tasmania, which "refuge" was not reached by *Neositta* and has, apparently, only recently been colonized by *Climacteris*. Neither *Neositta* nor *Platycercus* have developed forms on Eyre Peninsula and in the Hamersley region of the mid-west. There are, however, parallels in other genera, e.g. *Eopsaltria australis rosinae* on Eyre Peninsula and *Coracina novae-hollandiae subpallida* and *Dacelo leachi cliftoni* in the Hamersley Ranges.

A correlation of the type outlined above is to be expected if the refuge theory be sound. It is also not surprising, in view of the different ecological requirements of the various genera and the operation of chance factors, that the correlation is not complete and some species have forms where others have not.

There is at present a certain amount of disagreement amongst zoologists as to whether the Australian continent has been materially, or only slightly, more arid in the recent past than at present. Tindale (1949) and Condon (1954) have taken the latter view, drawing attention to certain relict populations that would have been exterminated by much greater aridity than at present. The present study of *Climacteris* does not throw any light on this question. Secondary extensions of range, particularly that of *melanura*, indicate a moderate improvement in climate and corroborate the evidence from *Neositta* and other sources that the Australian continent is now somewhat less arid than in the immediate past.

VI. ACKNOWLEDGMENTS

This paper is the first of a series directed at an investigation of the speciation process in the continental bird fauna of Australia. The work had its origin in the United States of America and I would like to express my thanks to the administrators of Harvard University, the U.S. Educational Foundation, and the American Museum of Natural History, New York, whose scholarships and financial grants made it possible. I am indebted to Dr. E. Mayr for personal guidance, and to the American Museum for facilities afforded me whilst I worked on their magnificent collection of Australian and Pacific birds.

To the Trustees of the Australian Museum, Sydney, I owe a special debt for the granting of study leave, assistance, and encouragement. The Directors and ornitho-

logists of the National Museum, Melbourne, and South Australian Museum, Adelaide, have given me the greatest assistance whilst I worked on their collections. Mr. B. Bertram, Australian Museum Department of Design, was an invaluable aid in preparing illustrations.

VII. REFERENCES

- AMADON, D. (1943).—Bird weights as an aid in taxonomy. *Wilson Bull.* 55: 164.
- ASCH, (1926).—"Official Check-list of the Birds of Australia." 2nd Ed. p. 90. (Govt. Printer: Melbourne.)
- BARNARD, C. A., and BARNARD, H. G. (1925).—A review of the bird life on Coomeroobalaroo Station, Duaringa district, Queensland. *Emu* 24: 263.
- BARNARD, H. G. (1926).—Birds of the Cardwell district. *Emu* 26: 1.
- BRECKY, F. L. (1905).—Birds of the Richmond district, Queensland. *Emu* 5: 75.
- BROWNE, W. K. (1945).—An attempted post Tertiary ornithology for Australia. *Proc. Linn. Soc. N.S.W.* 70: 5.
- CARR, A. J. (1955).—A revision of *Trichoglossus haematodus* and of the Australian platycercine parrots. *Ibis* 97: 432.
- CAMPBELL, A. J. (1961).—Another decade in Australian ornithology. *Emu* 3: 176.
- CAMPBELL, A. J. (1923).—Tree-creepers of the genus *Climacteris*. *Emu* 23: 1.
- CHISHOLM, A. H. (1945).—Birds of the Gilbert diary. *Emu* 44: 193.
- COMPTON, H. T. (1951).—Notes on the birds of South Australia: occurrence, distribution, and taxonomy. *S. Aust. Orn.* 20: 57.
- COMPTON, H. T. (1954).—Remarks on the evolution of Australian birds. II. The 'great and' hypothesis and refuge areas. *S. Aust. Orn.* 21: 17.
- CROCKER, R. L., and WOOD, J. G. (1947).—Some historical influences on the development of the South Australian vegetation communities and their bearing on concepts and classification in ecology. *Trans. Roy. Soc. S. Aust.* 71: 91.
- GENTILI, J. (1949).—Foundations of Australian bird geography. *Emu* 49: 23.
- HOWE, F. E. (1921).—The genus *Climacteris* (tree-creepers). *Emu* 21: 32.
- JAMES, H. E. A. (1944).—The birds on Barka Barka Station, Northern Territory of Australia. *S. Aust. Orn.* 17: 28.
- KEAST, A. (1956).—Variation in the Australian Oriolidae. *Proc. R. Zool. Soc. N.S.W.* 1956: 19.
- MACGILLIVRAY, W. (1914).—Notes on some north Queensland birds. *Emu* 13: 132.
- MACGILLIVRAY, W. (1929).—Through a drought stricken land. *Emu* 29: 125.
- MOCK, G. (1903).—Birds from Cape York peninsula, Queensland. *Mem. Qd. Mus.* 13: 23.
- MATTHEWS, A. J. (1933).—In search of a lost bird, with notes on other birds observed. *Emu* 32: 99.
- MATTHEWS, G. M. (1923).—The Birds of Australia. Vol. II, pp. 32 et seq. (H. F. and G. Witherby: London.)
- MAYR, E. (1941).—List of New Guinea Birds. p. 128. (American Museum of Natural History: New York.)
- MAYR, E. (1950).—Taxonomic notes on the genus *Neonitta*. *Emu* 49: 282.
- MAYR, E., and AMADON, D. (1951).—A classification of recent birds. *Amer. Mus. Novit.* No. 1496, p. 23.
- MAYR, E., and JARROLD, D. L. (1944).—The number of Australian bird species. *Emu* 44: 36.
- MCGILL, A. R. (1948).—A distributional review of the genus *Neonitta*. *Emu* 48: 33.
- PROBERT, J. A. (1931).—The soils of Australia in relation to vegetation and climate. *Comm. Sci. Industr. Res. Bull. Aust.* No. 52.
- STRECHER, D. L. (1951).—The evolution of the chestnut shouldered wrens (*Malurus*). *Emu* 51: 113.

SPECIES IN THE GENUS *LEUCOTRIS*

Adult female *Leucotris melanotos* (*Leucotris melanotos*) showing the characteristic habit of clinging vertically to trunks, also showing long, slender, golden-yellow tail. A number of insects and spiders have been seen on the back. (Photomicrograph by Mr. Lee.)

- SERVENTY, D. L., and WHITTELL, H. M. (1951).—"A Handbook of the Birds of Western Australia." pp. 306 et seq. 2nd Ed. (Patersons Press: Perth.)
- SHARLAND, M. (1945).—"Tasmanian Birds: How to Identify Them." p. 101. (Oldham, Beddome, and Meredith: Hobart.)
- TERRILL, S. E., and RIX, C. E. (1950).—The birds of South Australia, their distribution and habitat. *S. Aust. Orn.* 19: 91.
- TINDALE, N. B. (1949).—New Satyridae cf the genus *Oreixenica* from South Australia and New South Wales, together with notes on the recent climate of South Australia. *Rec. S. Aust. Mus.* 9: 143.
- WHITLOCK, F. L. (1924).—Journey to central Australia in search of the night parrot. *Emu* 23: 276.
- WOLSTENHOLME, H. (1925).—Notes on the birds observed during the Queensland congress and camp-out, 1924. *Emu* 24: 249.

THE GENERA *HAPATESUS* CANDÈZE AND *TOORONGUS*. GEN. NOV.
(COLEOPTERA : ELATERIDAE)

By A. NEBOISS*

[Manuscript received June 6, 1957]

Summary

This paper deals with the systematics of two elaterid genera—*Hapatesus* Candèze and *Toorongus*, gen. nov. Both are characterized, and all species figured.

The genus *Hapatesus* is divided into two subgenera: *Hapatesus* s.s., with 11 species, of which eight are new and *Minutesus*, subgen. nov., with five species of which four are new. This division is based on differences in characters of the male and female genitalia. *H. leai* Schenkling is synonymized with *H. minor* (Lea), the latter being given specific rank. *H. bubanus* is a new name for *H. hirtus* var. *minor* Elston non Lea.

The genus *Toorongus* contains four species of which two are new. *H. dubius* Schwarz is synonymized with *T. jugulatus* (Candèze).

INTRODUCTION

The Australian elaterid fauna has attracted very little attention during the last twenty or thirty years. Though the number of specimens in collections is often quite large, those accurately identified are comparatively few. This is probably due to the fact that many of the type specimens have been deposited in overseas museums, and so have not been readily available for study by local entomologists.

A check list of the described species, and synonyms, with a bibliography of the family was published by the author (1956).† The present paper deals with the systematics of two closely related genera—*Hapatesus* Candèze and *Toorongus*, gen. nov., both belonging to the subfamily Ctenicerinae.

Apart from the more generally used morphological characters, the author paid particular attention to those of the genitalia. These are used extensively for separation at the specific level. A number of publications dealing with this subject has been consulted (Sharp and Muir 1912; Snodgrass 1935; Crowson 1955; Becker 1956). and from these the undermentioned terminology has been selected for use in this study. In the male, only the aedeagus is illustrated (Fig. 7), all soft internal parts being omitted. Terms adopted for the male genitalia are as follows:

Aedeagus—the median lobe and tegmen together.

Tegmen—term applied to the lateral lobes and basal piece together.

Lateral lobes (*L*)—the distal portion of the tegmen, forming two free processes laterally of the median lobe and enveloping it.

Basal piece (*B*)—basal portion of the tegmen.

*National Museum of Victoria, Melbourne.

†It is necessary to draw attention to the following change in the check list of Australian Elateridae, p. 64: genus *Patricia* Zwaluwenburg is preoccupied by Fox, 1940 (Lepidoptera: Nymphalidae) and should be changed to *Patriciella* Zwaluwenburg, 1953, Proc. Hawaii Ent. Soc. 15: 20.

Median lobe (*M*)—the central portion of the aedeagus.

Apical hook (*AH*)—hook on the external edge of the lateral lobe near the distal end.

Apical section (*AS*)—transparent section of the lateral lobe at the distal end.

Shoulder (*S*)—the tapered basal portion of the median lobe.

Furca (*F*)—the two basal processes of the median lobe.

In the females it was found that the spiny plate or lamina dentata on the bursa copulatrix in the subgenus *Hapatesus* (Fig. 19), with additional patch of spiculation on the walls of bursa copulatrix near the opening of the spermathecal duct in the subgenus *Minutesus* (Fig. 31) and chitinous spines on the spermathecal duct (Fig. 40) in the genus *Toorongus* are good taxonomic characters.

The taxonomic importance of the reproductive organs, especially the lamina dentata of the female, was realized independently by Becker (1956) and by the present author. Although these organs have long been known to entomologists, Becker's paper on the genus *Agriotes* is the first in which use is made of them for taxonomic purposes.

Until the present work only one species of *Hapatesus* was known outside Australia. Recently examined material contained some undescribed species from New Guinea and New Britain, which will be described in a separate paper. Apart from these, there is only one record known to the author of an Australian species being found elsewhere, that being the record of *H. hirtus* Candèze from Formosa by Miwa (1928). No specimen from this area has been examined.

Both genera are distributed over a narrow belt, some 200–250 miles in width, along the eastern and south-eastern seaboard of the continent (Figs. 1, 26, 36). The localities in northern Queensland fall into areas where some tropical rain-forests are present; even near Normanton, Qld., there are pockets of rain-forest along the creeks. Distribution in the southern states is associated with wet eucalypt forests, and more or less mountainous country.

The early stages of *Hapatesus* and *Toorongus* are not yet known; Lea (1908, p. 157) mentioned that adults of *H. minor* (Lea) at King I. had been found near the roots of littoral plants on which he surmised the larvae might be feeding.

Material has been received from the following institutional and private collections. Abbreviations by which the collections are referred to in the text are also given.

Institutions

AM	Australian Museum, Sydney.
BM	British Museum (Natural History), London.
BPM	Bernice P. Bishop Museum, Honolulu.
CSIRO	Division of Entomology Museum, C.S.I.R.O., Canberra.
DEI	Deutsches Entomologisches Institut, Berlin.
HM	Tasmanian Art Gallery and Museum, Hobart.
HSPA	Hawaiian Sugar Planters Association, Honolulu.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels.
MACL	Macleay Collection, University of Sydney.
NM	National Museum of Victoria, Melbourne.

NSWDA	New South Wales Department of Agriculture, Sydney.
QM	Queensland Museum, Brisbane.
QU	Queensland University, Brisbane.
SAM	South Australian Museum, Adelaide.
SM	Naturhistoriska Riksmuseum, Stockholm.
TDA	Tasmanian Department of Agriculture, Hobart.
VDA	Victorian Department of Agriculture, Burnley, Vic.

Private Collections

AS	Smith, A., Melbourne.
CD	Deane, C., Caloundra, Qld.
ETS	Smith, E. T., Melbourne.
FEW	Wilson, F. E., Melbourne.
FH	Hallgarten, F., Melbourne.
JA	Armstrong, J., Nyngan, N.S.W.
JB	Balderston, J., Sydney.
JGB	Brooks, J. G., Cairns, Qld.
JK	Kissane, J., Melbourne.
JS	Sedlacek, J., Cooma, N.S.W.

Genus HAPATESUS Candèze

Hapatesus Candèze, 1863, Mem. Soc. Sci. Liège 17:188.

Hapatesus, Schwarz, 1907, Gen. Ins. 46:233.

Type species *Hapatesus (Hapatesus) hirtus* Candèze.

This genus was erected by Candèze for a single species from Australia, and other species were added in subsequent years. Schwarz (1902) noticed differences in the lengths of the 2nd and 3rd antennal segments and further study in this group shows a number of other differences which permit the removal to a new genus of two species previously included here. *Hapatesus* itself clearly falls into two subgenera.

Head comparatively small, fine to moderately punctate; frons with a more or less deep triangular median depression, bordered along the epicranial suture. Mandibles moderately curved, bearing a tooth near apex. Maxillary palps with terminal segment hatchet-shaped. Antennae short, 1st segment thickened, 2nd segment longer than 3rd, succeeding ones short and triangular, last elongate.

Pronotum short, moderately punctate, with more or less clearly marked median line; sides either gradually narrowed, or else parallel at rear and then more or less abruptly contracted toward anterior angles; posterior angles short, acute; carina extending as far as anterior angles.

Elytra with well-defined striae, intervals usually flat, finely punctate.

Legs short, tarsi simple, segments 1-4 diminishing in length, pilose beneath. The posterior coxae have a distinct hook on the posteromedian portion, as shown in Figure 5.

KEY TO SUBGENERA OF THE GENUS HAPATESUS

- | | |
|---|----------------------------------|
| 1. Lateral lobe of aedeagus with apical hook, bursa copulatrix without apiculation | <i>Hapatesus</i> , n. s. |
| Lateral lobe of aedeagus without apical hook, bursa copulatrix with apiculation near opening of the spermathecal duct | <i>Menestheus</i> , subgen. nov. |

Subgenus HAPATESUS, s.s.

Type species *Hapatesus (Hapatesus) hirtus* Candèze.

As indicated in the key, this subgenus is segregated by the distinct male and female characters. The lateral lobes of the aedeagus bear more or less strongly developed apical hooks which, with the apical sections, are important for separation at the specific level. In the females a well-developed pair of spiny plates, or lamina dentata, are situated within the walls of the bursa copulatrix.

This subgenus has the wider range of the two, extending from the islands north of Australia along the eastern seaboard of the continent, to just beyond the Victorian-South Australian border in the south-west (Fig. 1).



Fig. 1.—Map showing distribution of species of the subgenus *Hapatesus*.

KEY TO SPECIES OF THE SUBGENUS HAPATESUS

1. Pronotum very shiny, sparsely and finely punctate New Guinea and New Britain species
Pronotum not so shiny, due to denser and coarser punctation Australian species. 2
- 2(1). Pronotum and elytra concolorous 3
Pronotum orange, elytra darker reddish brown *H. (H.) kershawi*, sp. nov.
- 3(2). Pronotum and elytra covered with concolorous hairs 4
Pronotum and scutellum densely covered with golden hairs, elytra less densely with silvery hairs *H. (H.) argentatus*, sp. nov.
- 4(3). Pronotum and elytra densely covered with rich golden hairs 5
Hairs less dense, silvery, creamy, or yellowish, but never rich golden 7
- 5(4). Hairs on the elytra arranged longitudinally along the middle of intervals
..... *H. (H.) tepidus*, sp. nov.
Hairs arranged in oblique cross lines 6

- 6(5). Basal piece with inner posterior margin V-shaped; lamina dentata pear-shaped *H. (H.) pretiosus* Cand.
 Basal piece with inner posterior margin semicircular; lamina dentata obtusely reniform *H. (H.) zonatus*, sp. nov.
- 7(4). Pronotum strikingly convex; almost black species covered with silvery hairs *H. (H.) globosus*, sp. nov.
 Pronotum not strikingly convex 8
- 8(7). Species 12 mm or longer, robust 9
 Species 10 mm or smaller, slender 10
- 9(8). Aedeagus with lateral lobe apical hook small; lamina dentata with large spines extending beyond the dorsal edge *H. (H.) opulentus*, sp. nov.
 Aedeagus with lateral lobe apical hook large; lamina dentata with medium-sized spines, none of them extending beyond the dorsal edge *H. (H.) hirtus* Cand.
- 10(8). Aedeagus with median lobe spatulate *H. (H.) electus*, sp. nov.
 Aedeagus with median lobe not spatulate 11
- 11(10). Aedeagus robust; species from King I. and Tasmania *H. (H.) minor* (Lea)
 Aedeagus slender; species from south Queensland and New South Wales *H. (H.) junctus*, sp. nov.

HAPATESUS (HAPATESUS) KERSHAWI, sp. nov.

(Figs. 8, 9)

This species is easily separable by its distinctive colour. Head and antennae reddish brown; pronotum orange, with small punctures, covered with fine yellowish white or white hairs, anterior margin and posterior angles red-brown. Elytra red-brown, covered with yellowish white to white hairs, some of them semi-erect, striae slightly impressed, intervals flat, finely punctate. Legs orange-brown. Prosternum orange, metasternum and abdomen red-brown, punctures finer than those on pronotum, covered with yellowish white decumbent pubescence.

Aedeagus moderately slender, lateral lobes each with comparatively small apical hook. Median lobe slightly spatulate at the apex, furca short and rounded.

Lamina dentata small, oval, with very small spines.

Length 6.5–9 mm, width 1.5–2.5 mm.

Type material.—Holotype ♀: Narracan, Vic., Nov. 1896, W. Kershaw (NM); allotype ♂: Tebrabucca, N.S.W., 16.xi.1953, A. Neboiss (NM); 10 paratypes: 2 ♂♂, 1 ♀, Barrington Tops, N.S.W., H. J. Carter, and Sydney Univ. Zool. Exp. (AM); 2 ♀♀, Narracan, Vic., Nov. 1896, W. Kershaw, and 16.ii.1897, W. Kershaw (NM); 1 ♂, south Gippland, Vic., H. W. Duxey (SAM); 1 ♀, Camfield, Vic., 9.x.1918, F. E. Wilson (FEW); 2 ♀♀, 1 ♂, Mt. Donna Buang, Vic., 26.xii.1948, E. T. Smith (QM; ETS).

Distribution.—NEW SOUTH WALES; VICTORIA.

The species is dedicated to W. Kershaw, collector of the first specimens.

HAPATESUS (HAPATESUS) ARGENTATUS, sp. nov.

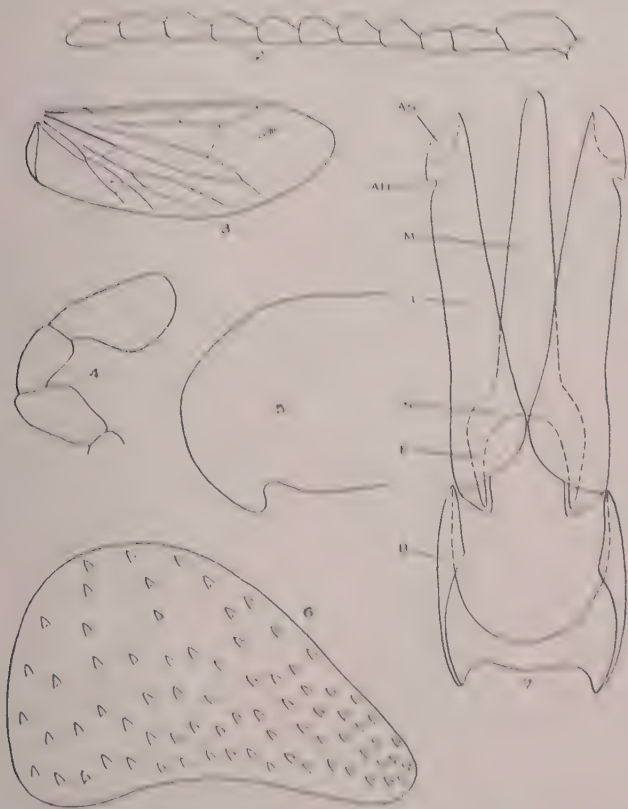
(Figs. 10, 11)

Hapatesus pretiosus Elston non Candèze, 1930, Ark. Zool. 22: 18.

This species, although close to *H. pretiosus* Cand., is easily separable by the sparse silvery hairs arranged along the striae on the elytra. A number of specimens bear Elston's identification labels with the name of *H. pretiosus* Cand., but comparison

of these specimens with the type of *H. pretiosus* Cand. has shown that they belong to a distinct species.

Head, pronotum, and elytra, as well as antennae and legs, dark reddish brown. Head, pronotum, and scutellum covered rather densely with golden, elytra with much sparser silvery hairs. Pronotum densely punctate with moderate punctures. Striae



Figs. 2-7.—*H. (H.) hirtus* Cand.: 2, antenna; 3, wing venation; 4, maxillary palp; 5, portion of posterior coxa; 6, lamina dentata; 7, aedeagus; *AH*, apical hook; *AS*, apical section; *B*, basal piece; *F*, furca; *L*, lateral lobe; *M*, median lobe; *S*, shoulder. *N.B.* Figures 6-18, 20-25, 17-30, 32-35, 40, and 42-35 are all of the same magnification.

on elytra rather deeply impressed, intervals flat with a row of irregularly placed fine punctures.

Ventral surface of the same dark red brown colour, moderately punctate, sparsely covered with fine silvery white hairs.

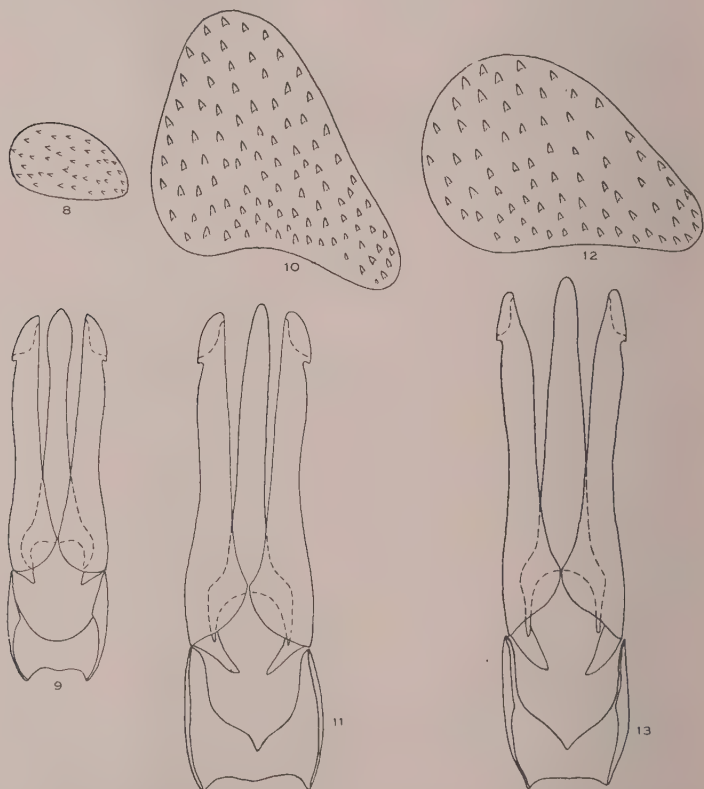
Aedeagus similar to that of *H. pretiosus*, but lateral lobes more slender, and posterior margin of the basal piece forming inside a V-shaped depression at centre.

Lamina dentata with highly raised dorsal margin, covered with moderately small spines, slightly smaller in central basal portion.

Length 9–11 mm, width 3–3.5 mm.

Type material.—Holotype ♀ and allotype ♂: Cairns district, Qld, A. M. Lea (AM); 15 paratypes: 1 ♂, Kuranda, Qld., F. P. Dodd (BM); 7 ♂♂ and ♀♀, Cairns district, Qld., A. M. Lea (AM; MACL; SAM; NM); 2 ♀♀, Malanda, Qld., Mjöberg (SM); 1 ♀, Atherton, Qld., Mjöberg (SAM); 1 ♀, Clump Point, Qld. (JS); 1 ♀, Richmond R., N.S.W., K. K. Spence (AM).

Distribution.—QUEENSLAND; NORTHERN NEW SOUTH WALES.



Figs. 8, 9.—*H. (H.) kershawi*, sp. nov.: 8, lamina dentata; 9, aedeagus. Figs. 10, 11.—*H. (H.) argentatus*, sp. nov.: 10, lamina dentata; 11, aedeagus. Figs. 12, 13.—*H. (H.) pretiosus* Cand.: 12, lamina dentata; 13, aedeagus.

HAPATESUS (HAPATESUS) PRETIOSUS Candèze

(Figs. 12, 13)

Hapatesus pretiosus Candèze, 1887, Notes Leyden Mus. 9: 287.

Re-examination of the holotype showed oblique arrangement of hairs on the elytra, their colour being golden and not silvery as stated in the original description. This error has no doubt been the cause of many misidentifications, and all those

specimens identified by Elston, so far as they have been available to the author for study, should be referred to *H. argentatus*.

Though closely related to *H. argentatus*, *H. tepidus*, and *H. zonatus*, this species is nevertheless easily separable from the former by the colour of the elytral hairs; from the second by the arrangement of these hairs; and from the latter by its smaller size, form of aedeagus, and lamina dentata.

Head, pronotum, and elytra very dark reddish brown, covered with golden hairs; antennae and legs lighter reddish brown. Head with slight depression in the middle, densely punctate. Pronotum unevenly punctate with moderate punctures, mostly separated by distances less than their diameters. There is a slight indication of a median furrow, which is more obvious near the posterior margin.

Elytra with moderately deep impressed striae, intervals uneven, punctures variable in size and density. Elytral hairs golden, arranged in oblique cross lines.

Ventral surface of the same colour as dorsum, moderately punctate, and covered with whitish decumbent pubescence.

Aedeagus slender, lateral lobes each with a moderately strong apical hook, interior margin bowed outwards near the apex.

Lamina dentata covered with moderately small spines.

Length 9–10.5 mm, width 3–3.5 mm.

Type material.—Holotype ♀: Normanton, Carpentaria Bay (IRSNB); ♂ genitalia drawn from a specimen collected at Tweed R., Qld. (SAM). Apart from the type another six specimens were available for study.

Distribution.—QUEENSLAND.

HAPATESUS (*HAPATESUS*) *TEPIDUS*, sp.nov.

(Figs. 14, 15)

This species resembles *H. pretiosus*, but differs in that the golden elytral hairs are not arranged in oblique cross lines, but cover the elytra evenly along the striae.

Both sexes are unicolorous dark reddish brown. Head and pronotum densely covered with golden hairs, punctate with moderate punctures. Elytra with deeply impressed striae, intervals flat with one row of punctures; covered with golden hairs.

Ventral surface finely punctate and covered with fine whitish decumbent pubescence.

Aedeagus not so slender as in *H. pretiosus* and *H. argentatus*, differing mainly in the shape of basal piece, especially in its narrow posterior margin.

Lamina dentata is comparatively shorter and more rounded than in *H. pretiosus*, but with slightly larger spines.

Length 8.5–11 mm, width 2.5–3.5 mm.

Type material.—Holotype ♀: Bunya Mts., Qld. (2000 ft), 14.xii.1937, N. Geary (AM); allotype ♂: Nanango district, Qld., Nov. 1927, H. Hacker (QM); 2 paratypes: 1 ♂, National Park, Qld., Nov. 1920, H. Hacker (QM); 1 ♀, Acacia Plateau, N.S.W., J. Armstrong (NM).

Distribution.—SOUTHERN QUEENSLAND and NORTHERN NEW SOUTH WALES.

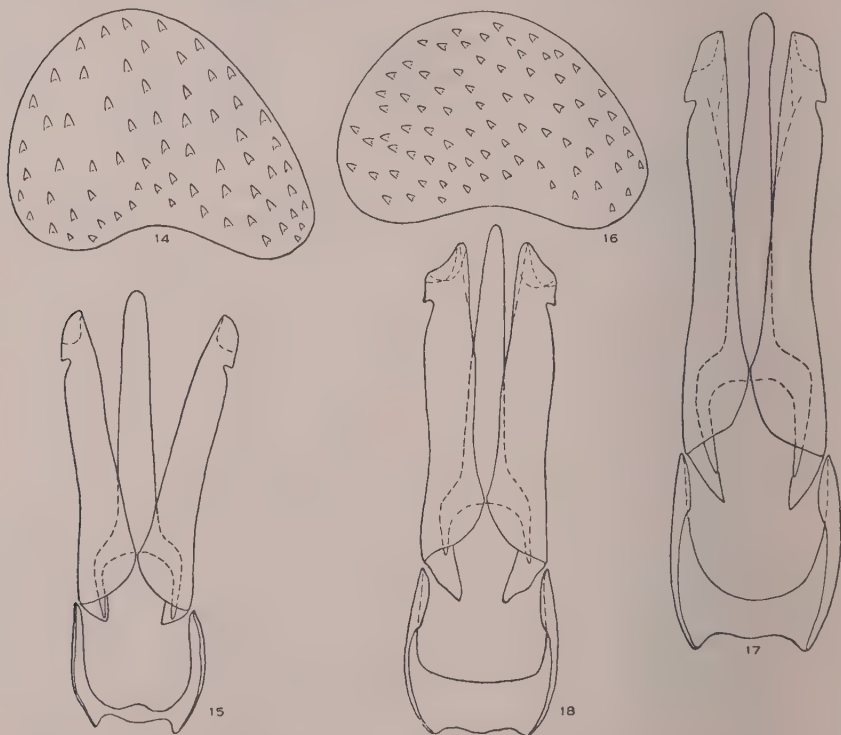
HAPATESUS (HAPATESUS) ZONATUS, sp. nov.

(Figs. 16, 17; Plate 1, Fig. 1)

This species resembles *H. pretiosus* in colour and in general appearance, but is distinctly larger.

Head and pronotum densely punctate with moderate punctures separated by less than their diameter, and covered with golden hairs. Elytra with moderately impressed striae, intervals punctate, the golden hair covering arranged in oblique cross lines. Legs and antennae dark reddish brown.

Ventral surface of the body dark reddish brown, covered with whitish decumbent pubescence, moderately punctate with fine punctures.



Figs. 14, 15.—*H. (H.) tepidus*, sp. nov.: 14, lamina dentata; 15, aedeagus. Figs. 16, 17.—*H. (H.) zonatus*, sp. nov.: 16, lamina dentata; 17, aedeagus. Fig. 18.—*H. (H.) globosus*, sp. nov., aedeagus.

Aedeagus with lateral lobes having a large well-developed apical hook. Median lobe slightly spatulate at the apex. Lamina dentata rounded, slightly longer than high, covered with moderately large spines.

Length 13–14.5 mm, width 4.4–5 mm.

Type material.—Holotype ♂: Acacia Plateau, N.S.W., J. Armstrong (JA); Allotype ♀: Dorrigo, N.S.W. (NM); 4 paratypes: 4 ♂♂, Acacia Plateau, N.S.W. (NM; JA).

Distribution.—NORTHERN NEW SOUTH WALES.

HAPATESUS (HAPATESUS) GLOBOSUS, sp. nov.

(Fig. 18)

Very dark reddish brown to black species, sparsely covered with silvery hairs. Legs and antennae of same colour as body, the latter being short, not extending as far as the posterior angles of prothorax. Pronotum and elytra strikingly convex, more so than in any other species in the genus. Head and pronotum densely punctate with moderately large punctures, elytra with moderately deep impressed striae, intervals rather wide, irregular punctures arranged in a single row.

Ventral surface sparsely covered with whitish decumbent pubescence, finely and sparsely punctate.

Aedeagus robust, with stoutly built lateral lobes. Apical hooks large and slightly concave. Median lobe straight.

Length 12 mm, width 4.5 mm.

♀. Unknown.

Type material.—Holotype ♂: Mackay, Qld. (NM).

Distribution.—NORTHERN QUEENSLAND.

HAPATESUS (HAPATESUS) OPULENTUS, sp. nov.

(Figs. 21, 22)

Specimens belonging to this species were usually found to be identified as *H. hirtus*, but they are generally larger and more robust in appearance; clearly separable from *H. hirtus* by the form of aedeagus and lamina dentata.

Head, pronotum, and elytra more or less uniformly dark reddish brown, covered with somewhat sparse semi-erect yellowish or whitish hairs. Pronotum moderately punctate, interspaces shiny, separated by distances usually more than their diameters. Intervals on the elytra flat, wide compared with striae, with one row of fine punctures. Striae rather shallow, especially along the median line and towards the apex.

Ventral surface of the same colour as dorsum, moderately punctate; pubescence decumbent, less dense than dorsally, yellowish white.

Aedeagus robust and large; lateral lobes slightly bent, rather wide, with small apical hook. Median lobe straight, with pointed apex.

Lamina dentata large with well-developed spines of unequal size and density.

Length 15–17 mm, width 4–5 mm.

Type material.—Holotype ♀: Mt. Evelyn, Vic., J. E. Dixon (NM); allotype ♂: Narara, N.S.W., 27.xi.1946, A. Burns (NM); 22 paratypes: 1 ♂, New South Wales (NM); 1 ♂, Narara, N.S.W., 27.xi.1946, A. Burns (NM); 1 ♀, Dorrigo, N.S.W., 12.xi.1911, R. J. Tillyard (QM); 3 ♂♂, 2 ♀♀, Cobbitty, N.S.W., Mar. 1934, K. K. Spence (AM); 2 ♂♂, 4 ♀♀, Jamberoo, N.S.W., Jan. 1949, N. W. Rodd (AM); 1 ♂, Illawarra, N.S.W., 4.x.1908, G. E. Bryant (BM); 1 ♂, Victorian Alps, Oct. 1902 (NM); 1 ♀, Warburton, Vic., 18.x.1903 (NM); 1 ♂, 1 ♀, Ferntree Gully, Vic., J. E. Dixon (NM); 2 + ♀♀, Gippsland, Vic. (NM; CSIRO); 1 ♀, Emerald, Vic., 7. iii.1954, J. Kissane (JK).

Distribution.—NEW SOUTH WALES, VICTORIA.

HAPATESUS (HAPATESUS) HIRTUS Candèze

(Figs. 2-7, 19; Plate 1, Fig. 2)

Hapatesus hirtus Candèze, 1863, Mem. Soc. Sci. Liege **17**: 188, pl. 2, fig. 8.

Somewhat flattened, uniformly dark reddish brown, sparsely covered with brownish yellow semi-erect hairs. Head with more or less triangular median depression, moderately punctate. Antennae short, the same colour as the body. Pronotum moderately punctate, with indication of a slight median furrow, posterior angles short, carina extending forwards as far as anterior angles. Elytra flattened

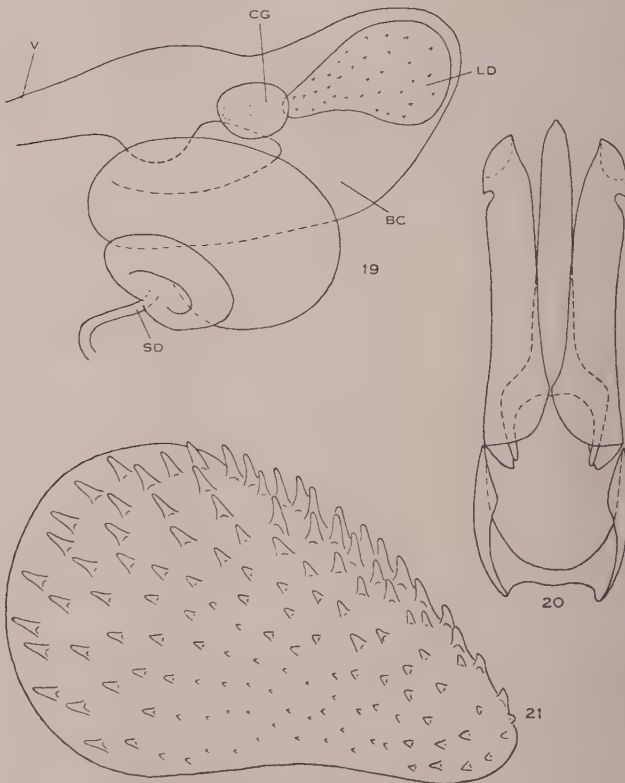


Fig. 19.—*H. (H.) hirtus* Cand., portion of female internal organs of reproduction: *BC*, bursa copulatrix; *CG*, colleterial gland; *LD*, lamina dentata; *SD*, spermathecal duct; *V*, vagina. Fig. 20.—*H. (H.) minor* (Lea), stat. nov., aedeagus. Fig. 21.—*H. (H.) opulentus*, sp. nov., lamina dentata.

along the median suture, striae straight and strongly punctate, especially the lateral ones. Intervals flat with one row of unequally spaced punctures. Ventral surface covered with decumbent yellowish brown pubescence.

Aedeagus strongly built, lateral lobes straight, each with large apical hook. Median lobe straight, evenly narrowed towards the apex.

Lamina dentata covered with medium-sized spines which are more or less densely arranged on the narrowed basal portion.

Length 11.5–14 mm, width 3.5–4.5 mm.

Type material.—Holotype ♀: Australia, without exact locality (IRSNB). Aedeagus drawn from a specimen collected on Victorian Alps (NM).

Distribution.—QUEENSLAND (near the southern border only); NEW SOUTH WALES; VICTORIA; SOUTH AUSTRALIA: Mt. Gambier, near Victorian border, at present the only known locality from this state.

Over 300 specimens were studied, and some variation in size and coloration was observed. Some pale orange-brown specimens were probably freshly emerged; others were very dark, nearly black. Examination of the male and female genitalia showed that these possessed rather stable characters.

This is the commonest species belonging to the genus *Hapatesus*. The most westerly records are from Mt. Gambier, S.A., and the Otway Ranges in western Victoria, and the most northerly ones from Acacia Plateau, N.S.W., and National Park, Qld., thus covering a region along the south-eastern coast of the continent.

A single female specimen from Nubeena, Tas. (in South Australian Museum collection), is doubtfully referred to this species. Lamina dentata appear to be slightly smaller and narrower than in typical *H. hirtus*; pronotum more elongate, elytra more convex, and intervals with irregular double rows of punctures. Should these and characters of the other sex, which is as yet unknown, prove to be constant, it might be necessary to separate it from *hirtus*.

HAPATESUS (HAPATESUS) MINOR (Lea), stat. nov.

(Fig. 20)

Hapatesus hirtus var. *minor* Lea, 1908, Proc. Roy. Soc. Vict. (N.S.) **20**: 157.

Hapatesus leai Schenkling, 1927, Col. Cat. **11** (88): 408.

Hapatesus leai Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 50.

Lea described King I. specimens as follows:

"The specimens from the island seem to represent a variety of this species, as they differ from typical ones in being smaller, with the clothing denser and longer, and the punctures in the elytral striae more pronounced; they also have the elytra more convex, and the median line of the prothorax more noticeable. I should probably have regarded them as belonging to a distinct species, but that a specimen before me has these differences even more pronounced, and was returned to me by Monsieur Candèze as var. *minor* of *hirtus*. One of the specimens was taken under bark, but seven others were taken at the roots of beech growing plants, and on which their larvae probably feed."

Schenkling (1927) proposed the name *Hapatesus leai* for the specimens from King I., but neither Lea nor Schenkling selected the type. Elston's description (1930) of *H. hirtus* var. *minor* from Queensland applies to another species—distinct from *H. hirtus* Cand. and *H. minor* (Lea)—see *H. bubanus*. Five of Lea's specimens were available for study and one of them is here selected as the lecto-holotype, and the other four as lecto-paratypes. There is a sixth specimen of this species, also a male, collected by Lea at Stanley, Tas. (SAM).

Uniformly reddish brown, covered with yellowish hairs. Elytra more convex than in *H. hirtus*, sides parallel, more or less abruptly narrowed at the apex. Prothorax and elytra of the same width.

Aedeagus similar to that of *H. hirtus* but shorter and stouter with lateral lobes more robust. Fork of the median lobe short.

Length 9.5–10.5 mm, width 3–3.5 mm.

♀. Unknown.

Type material.—Lecto-holotype ♂: King I., A. M. Lea (NM); lecto-paratypes: 4 ♂♂, King I., A. M. Lea (TDA, NM).

Distribution.—KING ISLAND; NORTHERN TASMANIA.

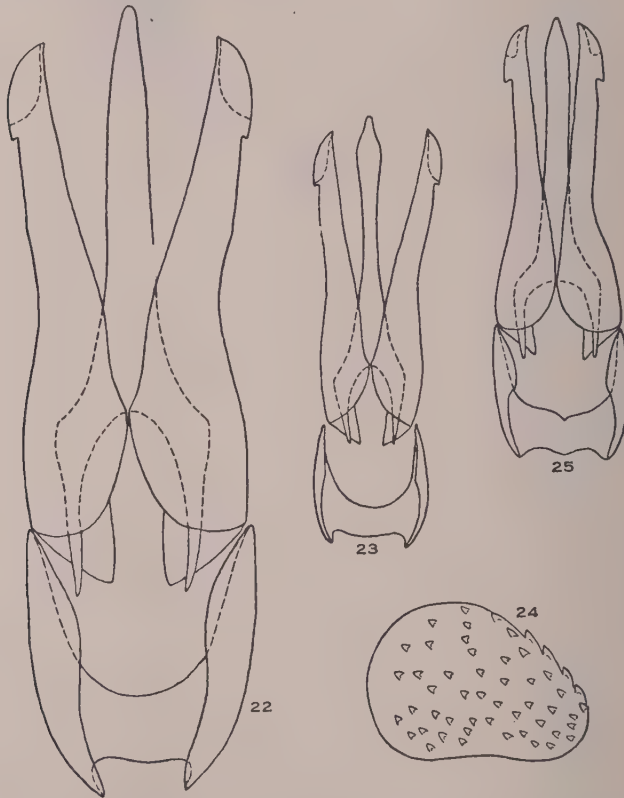


Fig. 22.—*H. (H.) opulentus*, sp. nov., aedeagus. Figs. 23, 24.—*H. (H.) electus*, sp. nov.: 23, aedeagus; 24, lamina dentata. Fig. 25.—*H. (H.) junctus*, sp. nov., aedeagus.

HAPATESUS (HAPATESUS) ELECTUS, sp. nov.

(Figs. 23, 24)

Uniformly reddish brown species, moderately covered with semi-erect, cream-coloured hairs. Head with triangular median depression moderately punctate, antennae extending slightly beyond the posterior angles of pronotum. Pronotum moderately punctate, with indication of slight median depression. Carina extending forward as far as anterior angles. Elytra slightly flattened along the median suture;

striae straight, moderately deep, punctate; intervals wide, flat, and partially covered with double, partially with single, rows of fine punctures, which are less distinct towards the apex.

Ventral surface finely punctate, covered with cream decumbent pubescence.

Aedeagus with median lobe spatulate, and pointed at the apex.

Lamina dentata similar to *H. bubanus*, but not quite so elongate. Some of the spines extend beyond the dorsal edge.

Length 7.5 mm, width 2.5–3 mm.

Type material.—Holotype ♀: Hornsby, N.S.W., May 1910, C. Gibbons (AM); allotype ♂: Hornsby, N.S.W., Oct. 1909, C. Gibbons (AM); 23 paratypes: 1 ♀, Queensland (NM); 1 ♂, Woolgoolga, N.S.W. (NM); 2 ♀♀, Upper Williams R., N.S.W., Oct. 1926, Lea and Wilson (FEW); 1 ♂, Chatswood, N.S.W., J. Armstrong (NM); 1 ♂, Hastings Range, N.S.W., J. Armstrong (JA); 1 ♂, Gosford, N.S.W. (SAM); 1 ♀, Epping, N.S.W., Nov. 1931 (AM); 1 ♀, Canterbury, N.S.W. (NM); 2 ♂♂, Hornsby, N.S.W., May 1910 (AM); 1 ♀, Young, N.S.W., Sloane (AM); 10 ♂♂ and ♀♀, Sydney, N.S.W. (MACL, NM, SAM, TDA); 1 ♀, National Park, N.S.W., Oct. 1908, G. E. Bryant (BM).

Distribution.—SOUTHERN QUEENSLAND; NEW SOUTH WALES.

HAPATESUS (*HAPATESUS*) JUNCTUS, sp. nov.

(Fig. 25)

Dark coffee-brown species, some specimens nearly black, covered with fawn-coloured, semi-erect hairs. Antennae and legs lighter reddish brown. Head moderately punctate, with slight depression in the middle. Pronotum moderately punctate, punctures approximately their diameters apart. Elytra with striae moderately impressed, less so along the median suture, intervals flat, covered with fine punctures in irregular rows.

Ventral surface moderately and finely punctate, covered with brownish yellow decumbent pubescence.

Aedeagus characterized by its distinct basal piece, posterior margin of the latter forming inside a distinct V-shaped depression at centre, but outside a rounded central lobe. Median lobe straight with pointed apex.

Length 9–10 mm, width 3 mm.

♀. Unknown.

Type material.—Holotype ♂: Northern New South Wales, J. Sedlacek (NM); 4 paratypes: 2 ♂♂, Acacia Plateau, N.S.W., J. Armstrong (JA, NM); 1 ♂, Bunya Mts., Qld., 10.xii.1925, H. Hacker (QM); 1 ♂, Gilgandra, N.S.W., J. Sedlacek (JS).

Distribution.—SOUTHERN QUEENSLAND; NEW SOUTH WALES.

Subgenus MINUTESUS, subgen. nov.

(Figs. 26, 31)

Type species *Hapatesus* (*Minutesus*) *bubanus*, nom. nov.

This subgenus is separated from the typical subgenus *Hapatesus* by the differences in the genital characters. In the males, the aedeagus is of the same general pattern, but the lateral lobes are without apical hooks.

In the females, apart from the lamina dentata which is similar to those found in the subgenus *Hapatesus*, there is also more or less pronounced spiculation near the opening of the spermathecal duct at the base of bursa copulatrix (Fig. 31).

Five species are placed in this subgenus. Females are known for three species, of which one is represented by a single slightly damaged specimen, with part of bursa copulatrix missing. The females of *H. (M.) sagittarius*, sp. nov., and *H. (M.) gundus*, sp. nov., are unknown.

Species belonging to this subgenus have similar distributions to those of the subgenus *Hapatesus*, except that they do not occur as far south. The most southerly records are from the Dorrigo and Gosford districts, N.S.W. At the present time only one species, *H. (M.) pervulgatus*, sp. nov., is known from southern Queensland and New South Wales, whereas four species are represented in the northern areas.

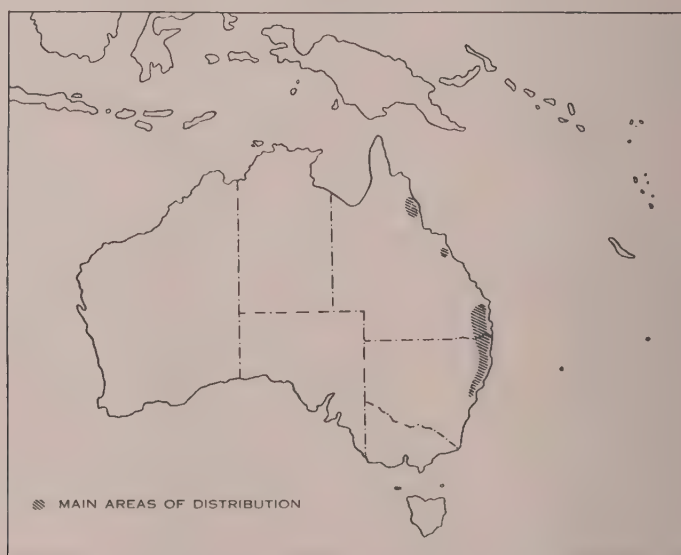


Fig. 26.—Map showing distribution of species of the subgenus *Minutesus*.

KEY TO SPECIES OF THE SUBGENUS MINUTESUS

1. Third segment nearly as long as second *H. (M.) gundus*, sp. nov.
Third antennal segment distinctly shorter than second 2
- 2(1). Pronotum and elytra covered with concolorous hairs 3
Pronotum covered with golden, elytra with silvery, hairs *H. (M.) sagittarius*, sp. nov.
- 3(2). Pronotum and elytra covered with fawn or creamy hairs 4
Pronotum and elytra covered with golden hairs *H. (M.) pervulgatus*, sp. nov.
- 4(3). Unicolorous rust brown species *H. (M.) pallidus*, sp. nov.
Dark reddish brown species, elytra with darker posterior third
..... *H. (M.) bubanus*, nom. nov.

HAPATESUS (MINUTESUS) SAGITTARIUS, sp. nov.

(Fig. 27)

Head almost black-maroon, covered with fine golden hairs, evenly punctate, depressed in the middle. Antennae reddish brown, 1st and 2nd segments slightly darker, in length reaching beyond the posterior angles of the prothorax. Pronotum dark maroon, moderately punctate, and covered with golden hairs. Elytra dark maroon, slightly darker along the edges, sparsely covered with silvery hairs. Striae moderately impressed, intervals almost flat, unevenly punctate. Legs reddish brown.

Ventral surface punctate, the same colour as dorsum, sparsely covered with silvery hairs.

Aedeagus with lateral lobes slender, sharply pointed at tips; median lobe slender, sharply pointed.

Length 9 mm, width 3 mm.

♀. Unknown.

Type material.—Holotype ♂: Malanad, Qld., Mjöberg (AM).

Distribution.—NORTH QUEENSLAND.

In shape and size this species closely resembles *H. (H.) argentatus*, but the aedeagus is completely different. It may also be distinguished by its less deeply impressed elytral striae, and its finer pronotal and elytral vestiture.

HAPATESUS (MINUTESUS) PERVULGATUS, sp. nov.

(Figs. 28, 29; Plate 1, Fig. 3)

This species has been confused with *H. bubanus* because of its very similar superficial appearance. Closer examination of the male and female genitalia, as well as the longer and golden hairs, makes it easily separable from the abovementioned species.

Head, pronotum, and elytra dark reddish brown, somewhat darker in colour than pronotum; covered with golden hairs. Pronotum wider than long; punctures dense, of moderate size, less than one diameter apart. Elytra with moderately impressed striae; intervals flat, wide, finely and irregularly punctate.

Punctures on the ventral surface of the body finer, and less dense, than on pronotum. Pubescence decumbent, fine and yellowish.

Aedeagus slender, lateral lobes straight and without apical hooks, median lobe straight, furca long and straight.

Lamina dentata oval, covered with comparatively small spines, these more or less uniform in size. Spiculation near the base of bursa copulatrix longer and more pronounced than in *H. bubanus*.

Length 7–8 mm, width 2.5–3 mm.

Type material.—Holotype ♂: New South Wales (NM); allotype ♂: Mt. Tamborine, Qld., Jan. 1912, H. J. Carter (NM); 17 paratypes: 4 ♂♂, Bunya Mts., Qld., 10.xii.1925, H. Hacker (QM); 1 ♂, National Park, Macpherson Range, Qld., 26.xii.1928, H. J. Carter (AM); 2 ♂♂, Brisbane (AM, QU); 2 ♀♀, 3 ♂♂, Tooloom, N.S.W., Jan. 1926, H. Hacker (QM); 1 ♂, Tweed R., N.S.W. (NM); 1 ♀, Ourimbah, N.S.W., 12.xi.1906 (DANSW); 1 ♀, Richmond R., N.S.W. (AM); 1 ♂, 1 ♀, New South Wales (NM).

Distribution.—QUEENSLAND; NEW SOUTH WALES.

HAPATESUS (MINUTESUS) GUNDUS, sp. nov.

(Fig. 30)

The colour is uniformly black, with exception of a small area enclosed within the posterior angles of the pronotum, which is dark brown; antennae and legs brown. Pubescence moderately dense, semi-erect, light fawn. Head moderately punctate with slight triangular depression in the middle. Pronotal punctures moderate, usually less than one diameter apart. Elytra with moderately deeply impressed striae, intervals flat with fine irregularly scattered punctures.

Ventral surface black, finely punctate, covered with fine brownish yellow decumbent hairs.

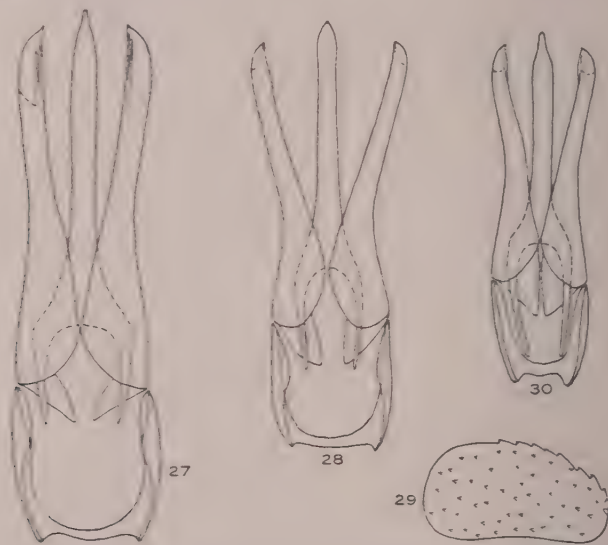


Fig. 27.—*H. (M.) sagittarius*, sp. nov., aedeagus. Figs. 28, 29.—*H. (M.) pervulgatus*, sp. nov.: 28, aedeagus; 29, lamina dentata.

Fig. 30.—*H. (M.) gundus*, sp. nov., aedeagus.

Aedeagus slender; median lobe straight, narrowed and pointed at apex, furca very long, nearly reaching posterior margin of the basal piece.

Length 7 mm, width 2.5 mm.

♀. Unknown.

Type material.—Holotype ♂: Cairns district, A. M. Lea (AM).

Distribution.—NORTH QUEENSLAND.

The trivial name "gunda", meaning "dark", is derived from an aboriginal word used by the natives from Walsh Creek (nr. Cairns), Qld.

HAPATESUS (MINUTESUS) PALLIDUS, sp. nov.

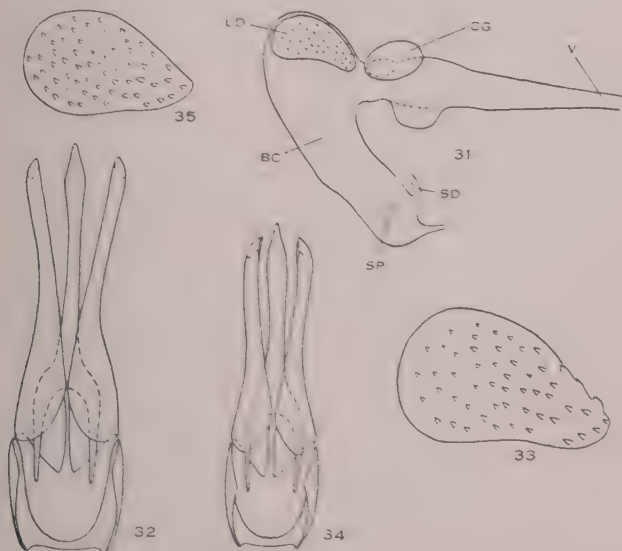
(Figs. 34, 35)

Uniformly rust brown species, moderately covered with yellowish semi-erect hairs. Head slightly depressed in the middle, and moderately punctate. Antennae

reaching just beyond the posterior angles of the prothorax. Anterolateral part of pronotum with a depression forming a slight triangular elevation in the centre of the anterior margin, finely punctate. Elytra with moderately impressed striae, intervals flat, finely and irregularly punctate.

Median lobe of the aedeagus sharply pointed, furca straight and long. Lateral lobes without apical hooks.

Lamina dentata pyriform, covered with comparatively small spines, slightly larger at the narrow end. The bursa copulatrix of the allotype is damaged by insect pests so it is not known whether spiculation is similar to that of *H. bubanus*.



Figs. 31-33.—*H. (M.) bubanus*, nom. nov.: 31, portion of female internal organs of reproduction: *BC*, bursa copulatrix; *CG*, colleterial gland; *LD*, lamina dentata; *SD*, spermathecal duct; *SP*, spiculation; *V*, vagina: 32, aedeagus; 33, lamina dentata. Figs. 34, 35.—*H. (M.) pallidus*, sp. nov.: 34, aedeagus; 35, lamina dentata.

Ventral surface finely punctate, covered with yellowish decumbent pubescence. Length 6-7 mm, width 2 mm.

Type material.—Holotype ♂, allotype ♀, and 1 paratype ♂: Mackay, Qld., NM; other paratypes: 1 ♂, Cairns, Qld., J. Sedlacek (JS); 1 ♂, Kuranda, Qld., 10.viii.1904 (HSPA).

Distribution.—NORTH QUEENSLAND.

HAPATESUS (MINUTESUS) BUBANUS, nom. nov.

(Figs. 31, 32, 33; Plate 1, Fig. 4)

Hapatesus hirtus var. *minor* Elston non Lea, 1930, Ark. Zool. 22: 19.

Hapatesus hirtus var. *minor* Neboiss, 1956, Mem. Nat. Mus. Vict. 22(2): 50.

The following is Elston's description:

"I have seen large number of specimens of the above and I am quite convinced they represent a small variety of *hirtus*. Lea (Proc. Roy. Soc. Victoria, 1907, p. 157) commented on this insect and, inter alia, mentioned that a specimen sent to Candèze for determination was returned by him labelled var. *minor* of *hirtus*. This name, apparently, was not published by Candèze and, as Lea (probably thinking that Candèze was publishing a note of this variety) passed it over, I now propose the above name. It agrees very well with *hirtus* in all respects except size, which varies from 6.5 to 8 mm in length; the elytra appear to be much more attenuated posteriorly.

Queensland: Bellenden Ker, Cedar Creek, Malanda. (Dr E. Mjöberg). Type in Stockholm Museum."

Elston apparently overlooked Schenkling's reference (1927) in "Coleopterorum Catalogus" where a new name, *H. leai*, was proposed for Lea's species from King I.; however, examination of Elston's type from the Stockholm Museum and its comparison with Lea's specimens from King I. showed that they belong to two different species.



Fig. 36.—Map showing distribution of species of the genus *Toorongus*.

Head, pronotum, and elytra dark reddish brown, covered with creamy semi-erect hairs, the elytra somewhat darkened on their posterior third. Dorsally covered with creamy semi-erect hairs. Punctures on pronotum moderately dense. Elytra with moderately impressed striae, intervals flat with one row of punctures.

Ventral surface dark reddish brown, finely punctate, covered with fine creamy decumbent pubescence.

Median lobe of the aedeagus spatulate, extreme apex pointed, furca straight and long. Lateral lobes smooth and without apical hooks.

Lamina dentata covered with medium-sized spines, which are slightly larger at the base. There is a small patch of fine spiculation near the opening of the spermathecal duct at the base of bursa copulatrix.

Length 6.5 mm, width 2-2.5 mm.

Type material.—Holotype ♂ (designated by Elston, 1930): Bellenden Ker, Qld., Mjöberg (SM); allotype ♀: Bellenden Ker, Qld., Mjöberg (AM); 13 paratypes: 1 ♀, Bellenden Ker, Qld., Mjöberg (AM); 2 ♀♀, Cedar Creek, Qld., Mjöberg (SM, AM); 1 ♀, Malanda, Qld., Mjöberg (SM); 2 ♂♂, Barron Falls, Qld., Koobelo (SAM); 5 ♀♀, 2 ♂♂, Cairns district, Qld., A. M. Lea (AM, NM).

Distribution. NORTH QUEENSLAND.

The trivial name "buban", meaning "little", is derived from an aboriginal word used by the natives from Weary Bay, Qld.

Genus *TOORONGUS*, gen. nov.

(Figs. 36-42)

Type species *Toorongus jugulatus* (Candèze), comb. nov.

This genus, although closely resembling *Hapatesus* Cand., is easily distinguished by the more pointed and elongate shape of the body, by the absence of a pronounced hook on the posterior coxa, and by the 2nd antennal segment being shorter than the 3rd. This latter character was noted by Schwarz (1902) when describing *H. dubius*, but he did not consider it sufficiently important to warrant the erection of a new genus.

The genus is characterized by the elongate shape of the body; head slightly convex or flat, anterolaterally with 2 punctiform depressions; antennae short, 2nd segment shorter than the 3rd, 4th and following segments short, triangular. Pronotum evenly convex, finely punctate; posterior angles short, straight; carina reaching anterior angles. Elytra with slightly to moderately impressed striae, intervals flat, indistinctly and sparsely punctate. Legs short, tarsi simple, posterior coxae narrowed outwardly, posteromedian portion with wide concavity.

The characters already discussed, together with the distinct form of the aedeagus, the presence of scattered chitinous spines along the spermathecal duct instead of lamina dentata on bursa copulatrix, and differences in the venation of the anal area of the wings (Fig. 41) are considered sufficient for regarding this group as generically distinct from *Hapatesus*.

The distribution of the genus *Toorongus* follows broadly the same lines as that of the genus *Hapatesus*, with the exception that it is contracted more to the north of the continent and to Tasmania. The most northerly records are from the Mt. Tamborine district in South Queensland. Specimens have been taken as far west as Portland, Vic. All available Tasmanian records are from northern and eastern localities.

The generic name is derived from an aboriginal word "toorong" meaning "new".

KEY TO SPECIES OF THE GENUS *TOORONGUS*

1. Striae on elytra moderately deep, at least moderately punctate 2
Striae shallow, not punctate or at most very finely and indistinctly punctate 3
- 2(1). Aedeagus robust, tips of the lateral lobes turned inward; spine on the spermathecal duct large, except at ends*T. jugulatus* (Cand.)
Aedeagus slender, lateral lobes straight; spermathecal duct with small spines only
.....*T. bivittus*, sp. nov.

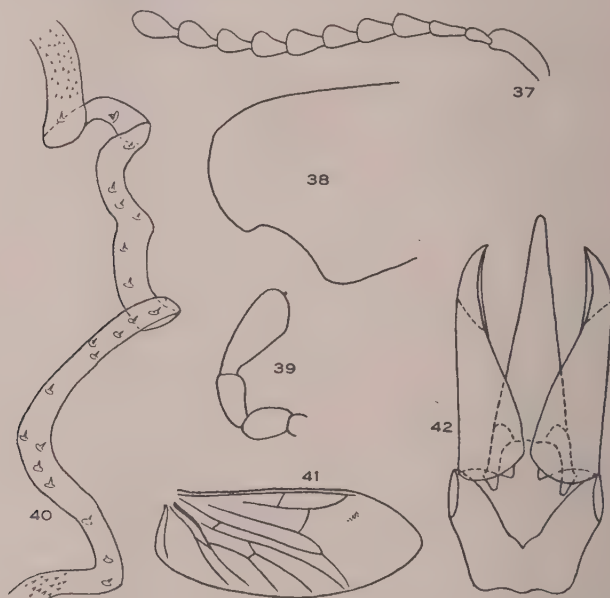
- 3(1). Length 8-9 mm; aedeagus with lateral lobes robust, apical section about one-third of the entire length; spermathecal duct with small scattered spines *T. excelsus* sp. nov.
 Length 4.5-6.5 mm; aedeagus with lateral lobes slender, apical section about one-eighth of the entire length; spines on spermathecal duct very small, less numerous
 *T. minutus* (Schw.)

TOORONGUS JUGULATUS (Candèze), comb. nov.

(Figs. 37-42)

Hapatesus jugulatus Candèze, 1900, Ann. Soc. Ent. Belg. **44**: 97.

Hapatesus dubius Schwarz, 1902, Dtsch. ent. Z. **1902**: 126 (syn. nov.).



Figs. 37-42.—*T. jugulatus* (Cand.): 37, antenna; 38, portion of posterior coxa; 39, maxillary palp; 40, spermathecal duct; 41, wing venation; 42, aedeagus.

The comparison of the type of *H. jugulatus* Cand. which is a female, and the type of *H. dubius* Schw., a male specimen, showed that they are opposite sexes of one species.

In the description of *jugulatus*, Candèze did not mention the lengths of the 2nd and 3rd antennal segments. Schwarz, when describing *dubius*, noted that the 2nd segment is very short, and gave this as one of the specific characters for separating *dubius* from *hirtus* and *jugulatus*. This is here regarded as one of the generic characters, because of its presence in all known species in the genus *Toorongus*.

Colour, although variable, is generally reddish brown. The body is moderately covered with semi-erect golden yellow hairs. Head almost flat, with 2 punctiform anterolateral depressions, unevenly, sparsely, and finely punctate. Pronotum as wide as long, sides gradually contracted from the base to anterior angles, evenly convex, glossy, with sparse, rather small, and shallow punctures. Carina parallel

to the sides, reaching the anterior angles. Elytra with striae moderately impressed, punctate; intervals flat, with a row of very fine punctures.

Ventral surface of the same colour as dorsum, sparsely punctate, covered with fine decumbent yellowish pubescence. Prosternum comparatively wide, rounded in front and produced forwards, visible dorsally.

Aedeagus strongly built, median lobe pointed, furca short and wide. Apex of the lateral lobes turned towards the centre. Basal piece wide, posterior margin lobed in the middle. Spermathecal duct covered with large chitinous spines, these being smaller and denser at either end of duct.

Length 8–12 mm, width 2.5–3.5 mm.

Type material.—Holotype ♀: Forest Reefs, N.S.W. (IRSNB); type ♂ of *H. dubius* Schw., Victoria, without exact locality (DEI), aedeagus figured from this specimen.

Distribution.—NEW SOUTH WALES, VICTORIA, TASMANIA.

Nearly 100 specimens from various localities were available for study.

Specimens from Mt. Tamborine, Qld., identified and described by Elston (1930) as *H. jugulatus* Cand. do not belong here, but are referred to *T. bivius* sp. nov., described below.

TOORONGUS BIVIUS, sp. nov.

(Fig. 43; Plate 1, Fig. 5)

Hapatesus jugulatus Elston non Candèze, 1930, Ark. Zool. 22: 18.

Almost uniformly light reddish brown species, margins of pronotum darker, sparsely covered with semi-erect golden yellow hairs. Head almost flat or slightly convex, anterolateral part with 2 punctiform depressions, finely and indistinctly punctate. Pronotum as wide as long, evenly convex, sparsely and finely punctate, sides contracting gradually in the posterior two-thirds, then more abruptly in the anterior third; carina reaching the anterior angles; posterior angles short. Elytra somewhat flattened, striae moderately impressed, punctate; intervals flat, with punctures sparse, fine, indistinct, and irregularly distributed.

Ventral surface finely punctate and covered with golden yellow pubescence. Prosternum wide, produced forwards, visible dorsally.

Aedeagus is very similar to that of *T. minutus* (Schw.), apart from its larger size. The median lobe is pointed at apex, the basal piece more elongate, and with internal margin more acutely V-shaped. Spermathecal duct with relatively few spines, these small and occupying the posterior half.

Length 7–8.5 mm, width 2–3 mm.

Type material.—Holotype ♂: Warburton, Vic., Jan. 1908 (NM); allotype ♀: Warburton, Vic., 18.x.1903 (NM); 4 paratypes: 1 ♀, Warburton, Vic., 6.xi.1904 (NM); 2 ♂♂, Woori Yallock, Vic., 28.i.1906 (NM, CSIRO); 1 ♂, Cabramurra, N.S.W., 4800 ft, 2.xii.1955, I. G. Fihner (QM).

Distribution.—SOUTHERN QUEENSLAND; NEW SOUTH WALES; VICTORIA.

A number of specimens from other localities are also referred to this species, although they appear to be more robust and larger in some cases, smaller in others, and have the prosternum less visible from above than in the type material. Examination of the genitalia failed to show distinctive characters justifying specific separation.

Four specimens from Mt. Tamborine, Qld., collected by Mjöberg (received from Stockholm Museum and Australian Museum), and identified by Elston as *H. jugulatus*, are referred to this species.

One specimen from Forest Reefs, N.S.W., in the collection of Institut Royal des Sciences Naturelles de Belgique, Brussels, labelled by Candèze as the type of *H. jugulatus* var. *minor*, also belongs to this species, but the name as used on the label apparently has never been published.

TOORONGUS MINUTUS (Schwarz), comb. nov.

(Fig. 45)

Hapatesus minutus Schwarz, 1903, Dtsch. ent. Z. **1903**: 395.

This is the smallest species of the genus *Toorongus*. It varies in colour from orange-brown to dark reddish brown, and is covered with semi-erect golden yellow

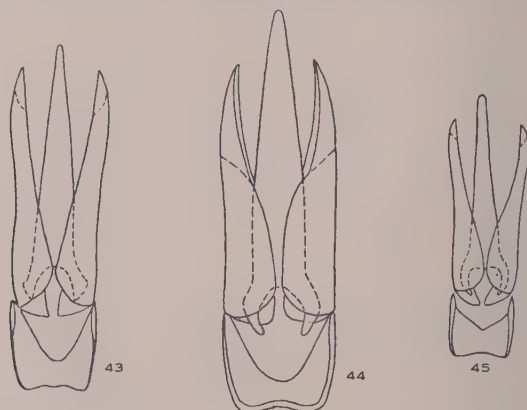


Fig. 43.—*T. bivius*, sp. nov., aedeagus. Fig. 44.—*T. excelsus*, sp. nov., aedeagus. Fig. 45.—*T. minutus* (Schw.), aedeagus.

hairs. Head almost flat, with sparse fine punctures, anterolateral part with 2 punctiform depressions. Antennae with 2nd segment shorter than the 3rd. Pronotum evenly convex, with sparse fine punctures, posterior angles straight, carina reaching anterior angles. Striae on the elytra shallow, not or only indistinctly punctate; intervals flat with an irregular row of very fine punctures.

Ventral surface of the same colour as dorsum, covered with fine decumbent hairs.

Median lobe of aedeagus with more or less rounded apex, furca small and circular. Posterior margin of the basal piece without a lobe in the middle. The spermathecal duct is sparsely covered with minute spines.

Length 4.5–6.5 mm, width 1.5–2 mm.

Type material.—Holotype ♂ and allotype ♀, Australia, without exact locality (DEI).

Distribution.—NEW SOUTH WALES, VICTORIA.

TOORONGUS EXCELSUS, sp. nov.

(Fig. 44)

This species is very similar to *T. jugulatus* and can only be identified with certainty by examination of the male and female genitalia.

All parts of the body including the legs and antennae are uniformly orange-brown, and covered with golden yellow hairs. Head with very fine punctures, and 2 strong punctiform depressions near the anterior margin. Antennae with 1st segment as long as the 2nd and 3rd together; 2nd segment short, 3rd longer. Pronotum carinate, with fine, sparse, rather shallow punctures. Elytra with shallow striae, intervals almost flat and indistinctly punctured.

Ventral surface finely punctate and covered with fine decumbent pubescence.

Aedeagus with strongly built median lobe, furca narrow and short. Lateral lobes with strong and pointed apex, apical section about one-third of the entire length. Basal piece small. Spermathecal duct sparsely covered with small spines.

Length 8-9 mm, width 2 mm.

Type material.—Holotype ♂: Island Bend, Mt. Kosciusko, N.S.W., 21-25.xi.1952, J. Armstrong (JA); allotype ♀: Mt. Buffalo, Vic., 4500 ft, 13.i.1955, A. Neboiss (NM); 2 paratypes: 1 ♂, Victorian Alps, Ejnar Fisher No. 748 (CD); 1 ♀, Nimmitabel, N.S.W., 23.ii.1951, F. E. Wilson, (FEW).

Distribution.—NEW SOUTH WALES; VICTORIA.

ACKNOWLEDGMENTS

I would like to express my sincere thanks to all abovementioned Institutions and collectors, for the loan of valuable material. For their kindness in making available type specimens in their care, I am especially indebted to Dr. J. M. Vrydagh, Institut Royal des Sciences Naturelles de Belgique, Brussels, to Dr. H. Sachtleben, Deutsches Entomologisches Institut, Berlin, and to Dr. R. Malaise, Riksmuseum, Stockholm. Acknowledgments are here made also to Dr. P. B. Carne, C.S.I.R.O., Canberra, and to Mr. R. A. Dunn, Melbourne, for their valuable criticism.

I have also to thank the other institutions and collectors who lent me material, but as no representatives of the two genera discussed in this paper were included, their names are not listed above.

REFERENCES

- BECKER, E. C. (1956).—Revision of the Nearctic species of *Agriotes* (Col. Elateridae). *Canad. Entom.* **88** (suppl. 1): 1-101.
- CROWSON, R. A. (1955).—"The Natural Classification of the Families of Coleoptera." (Nathaniel Lloyd & Co. Ltd.: London.)
- ELSTON, A. H. (1930).—Elateridae in results of Dr. E. Mjöberg's Swedish scientific expedition to Australia 1910-1913. *Ark. Zool.* **22**: 1-22.
- LEA, A. M. (1908).—The coleoptera of King Island, Bass Strait. *Proc. Roy. Soc. Vict.* (N.S) **20**: 143-207.
- MIWA, Y. (1928).—New and some rare species of Elateridae from the Japanese Empire. *Insecta matsum.* **2**(3): 133-46.
- NEBOISS, A. (1956).—A check list of Australian Elateridae, Coleoptera. *Mem. Nat. Mus. Vict.* **22**(2): 1-75.
- SCHENKLIING, S. (1927).—"Coleopterorum Catalogus." **11**(88): 407.

SCHWARZ, O. 1902.—Neue Elateriden aus Australien. *Dtsch. ent. Z.* 1902: 113-26.

SHARP, D., and MUIR, F. 1912.—The comparative anatomy of the male genital tube in Coleoptera. *Trans. Ent. Soc. Lond.* 1912: 477-642.

SNOODGRASS, R. E. 1935.—"Principles of Insect Morphology." (McGraw Hill Book Co.: New York.)

EXPLANATION OF PLATE I

Photographs by the author

Fig. 1.—*H(H.) zonatus*, sp. nov., ♂, holotype, Acacia Plateau, N.S.W.

Fig. 2.—*H(H.) hirtus* Cand., ♀, Kinglake, Vic.

Fig. 3.—*H(M.) pervulgatus*, sp. nov., ♂, paratype, Tweed R., N.S.W.

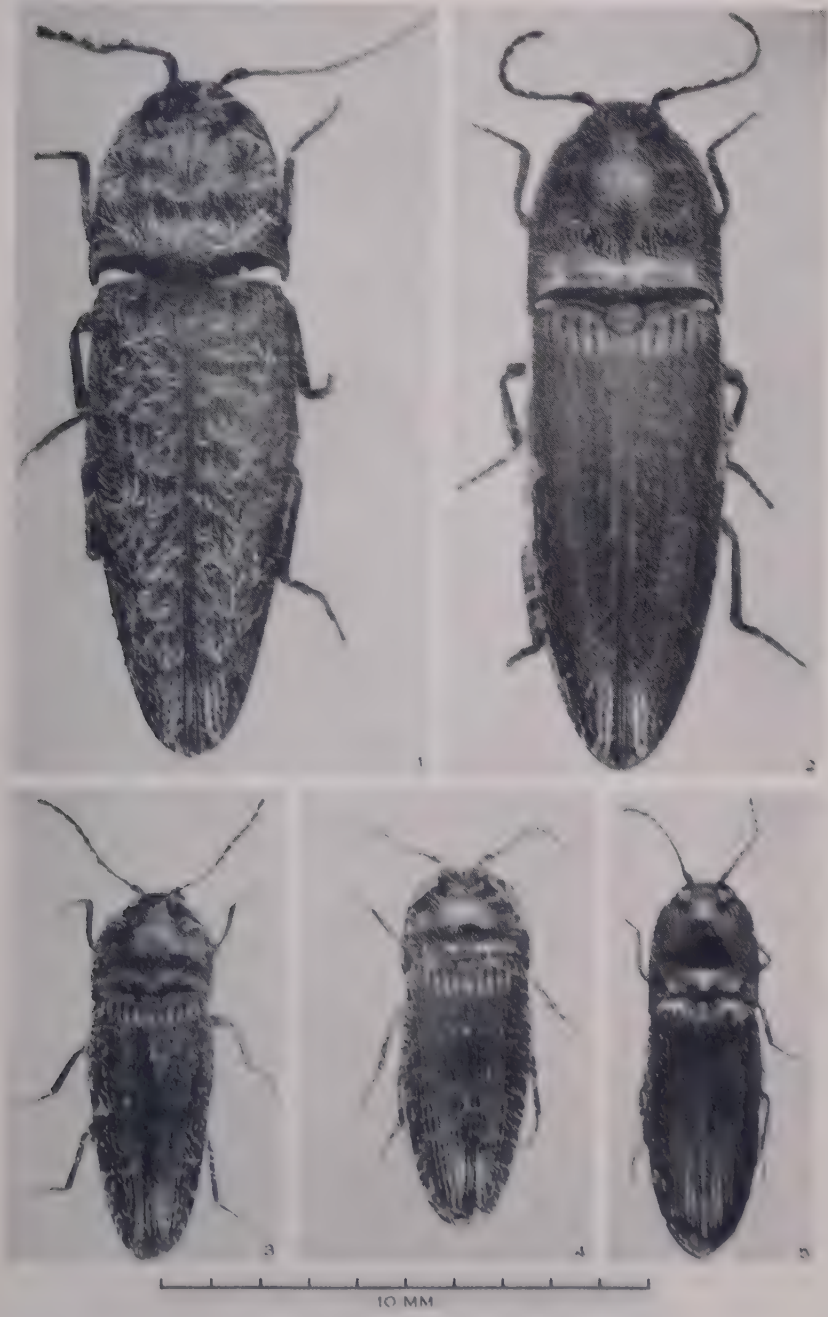
Fig. 4.—*H(M.) bubanus*, nom. nov., ♀, paratype, Cairns, Qld.

Fig. 5.—*T. bivius*, sp. nov., ♂, holotype, Warburton, Vic.

LIST OF SPECIES

	Page		Page
Subgenus <i>Hapaterus</i> , s.s.	499	<i>tepilus</i> , sp. nov.	503
<i>argentatus</i> , sp. nov.	500	<i>zonatus</i> , sp. nov.	504
<i>dubius</i> Schw.—see <i>Toorongus jugulatus</i> (Cand.)		Subgenus <i>Minutenus</i> , subgen. nov.	509
<i>electus</i> , sp. nov.	508	<i>bubanus</i> , nom. nov.	513
<i>globosus</i> , sp. nov.	505	<i>gundus</i> , sp. nov.	512
<i>hirtus</i> Cand.	506	<i>minor</i> Elston—see <i>H. (M.) bubanus</i> , nom. nov.	
<i>jugulatus</i> Cand.—see <i>Toorongus jugu-</i> <i>latus</i> (Cand.)		<i>pallidus</i> , sp. nov.	512
<i>junctus</i> , sp. nov.	509	<i>pervulgatus</i> , sp. nov.	511
<i>kershawi</i> , sp. nov.	500	<i>sagittarius</i> , sp. nov.	511
<i>leai</i> Schenk.—see <i>Hapaterus minor</i> (Lea)		Genus <i>Toorongus</i> , gen. nov.	515
<i>minor</i> (Lea), stat. nov.	507	<i>bivius</i> , sp. nov.	517
<i>minutus</i> Schw.—see <i>Toorongus minutus</i> (Schw.)		<i>excellus</i> , sp. nov.	519
<i>opulentus</i> , sp. nov.	505	<i>jugulatus</i> (Cand.)	516
<i>pretiosus</i> Cand.	502	<i>minutus</i> (Schw.)	518

REVISION OF THE GENERA HAPATESUS AND ECHINOCUS



A REVIEW OF AUSTRALIAN ACRO CERIDAE (DIPTERA)

By S. J. PARAMONOV*

[Manuscript received May 28, 1957]

Summary

Four genera and 26 species of Australian Acroceridae are recognized. The genus *Nothra* Westw. is synonymized with *Pterodontia* Gray. One new species of *Pterodontia* and 10 new species of *Oncodes* Latr. are described. It is indicated from structural studies that Hardy (1940) erroneously regarded all Australian species of *Oncodes* as only colour varieties of *O. basalis* (Walk.).

INTRODUCTION

The Australian Acroceridae (Cyrtidae olim) are very poorly known and in Australian Museums are represented chiefly by odd specimens. Hardy (1922) published data on all known Australian genera and species of this family. During the last 35 years new species were described only in the genus *Oncodes* Latr. (Brunetti 1926), but Hardy (1940) regarded them and those described by earlier authors as colour variations of *O. basalis* (Walk.).

The limits of the genera have been found to require redefinition. New species and data regarding previously described species have accumulated and the failure of Hardy to detect characters led to complete confusion in the genus *Oncodes*. These considerations induced the author to review the Australian representatives of the family anew, in spite of the limited material available.

Acroceridae is the oldest proposed family name, and, hence, is technically correct under the International Rules. It dates from Leach, 1815 (Acroceridae) and Samouelle, 1819 (Acroceridae), whereas Cyrtidae dates from Newman, 1834 (Cyrtites). Oncodidae and others are even more recent names and hence even less valid.

The Australian Acroceridae are represented now by four genera: *Leucopis* (1 species), *Pumpes* (3 species), *Pterodontia* (3 species), and *Oncodes* (19 species — 26 species in all).

CHARACTERISTICS OF THE FAMILY

Orthorrhaphous, brachycerous, eremochaetous flies, with 3 palvilli. Usually of medium size, head hidden by large humped thorax, abdomen inflated; lower calypter relatively gigantic.

Head very small or even minute, covered by thorax, and in some forms invisible from above; surface almost wholly occupied by the enormous eyes in both sexes, eyes smaller in female than in male but always holoptic in both sexes. Face very small, placed almost on underside of the head. Head entirely without bristles. Occiput with short hairs. Ocelli: 3, 2, or absent.

* Division of Entomology, C.S.I.R.O., Canberra.

Proboscis very variable between species, sometimes exceedingly long, directed backwards and nearly reaching the end of abdomen, or very short, or quite absent. Palpi usually obsolete.

Eyes bare or hairy; facets all equal in both sexes. Antennae 3-jointed, placed at extreme top near ocelli, at extreme bottom against the mouth, or, rarely, at about the middle of head. Third antennal joint without any style or arista (Panopinae), or with 3 apical hairs (*Pterodontia*), or itself elongated, arista-like.

Thorax very gibbous, bristleless, usually with short erect hairs. Vestiture of scutellum like that of thorax. Prothoracic lobes enormously developed in Philopotinae (this subfamily is absent from Australia).

Abdomen very broad, globose, sometimes pellucid. Hairs usually of moderate length. Genitalia small, inconspicuous in both sexes.

Legs simple, never long nor thin, entirely without bristles but sometimes with a short, blunt spur on the middle tibiae. Empodium pulvilliform.

Wings diverging and deflexed when at rest so that they lie against the abdomen. Venation very different in different genera. As a rule it is characterized by simplification or even disappearance of many veins. In *Oncodes* only traces of many veins remain.

LIFE HISTORY

The metamorphoses of a few species are known. The author thinks it best to give here a list of authors who have written on the subject:

Genera or Species	Reference
<i>Oncodes pallipes</i> Latr.	Mengo, 1866, <i>Schr. nat. Ges. Danzig</i> 1 : 37.
<i>Oncodes fumatus</i> Erichs.	Brauer, 1869, <i>Verh. zool.-bot. Ges. Wien</i> 19 : 737.
<i>Astomella lindeni</i> Erichs.	Brauer, 1869, <i>Verh. zool.-bot. Ges. Wien</i> 19 : 737, pl. 13, figs. 1-6. Brauer, 1883, <i>Denkschr. Akad. Wiss. Wien</i> 47 : pl. 5, figs. 89-92.
<i>Henops brunneus</i> Hutton	Maskell, 1888, <i>Trans. Proc. N.Z. Inst.</i> 20 : 106.
<i>Oncodes</i> sp.	König, 1894, <i>Verh. zool.-bot. Ges. Wien</i> 44 : 163.
<i>Oncodes</i> , life history	Locket, 1930, <i>Entomologist</i> 63 : 241. Milot, 1938, <i>Bull. Soc. Zool. Fr.</i> 63 : 162-81, 183-97, 14 figs.
<i>Oncodes pallipes</i> , early stages	Foytaud, 1947, <i>Rev. Ent. Fr.</i> 13 : 141, figs.
<i>Oncodes</i> larva	Plomley, 1947, <i>Rec. Q. Vict. Mus.</i> 2 : 26.

The most detailed data about the life history of Australian Acroceridae have been given by Plomley (1947a). The author has seen all material collected by Mr. Plomley, and can state that he was dealing not with *O. basalis* (Walk.), as he thought, but with *O. pygmaeus* White and *O. flavescens* White, which are probably synonyms of *O. fortnumi* Westw. Thus all information, illustrations, etc. in Plomley's paper concern not *O. basalis*, but *O. fortnumi*. Another article by the same author (1947b), must also be regarded as concerning *O. fortnumi*.

Adults. The adult flies are generally rare in collections, but there are indications that in nature they are sometimes very numerous, especially the genus *Oncodes*.

species of which have been reported by some observers in enormous numbers on the leaves of trees. Unfortunately the author, in the course of about 40 years collecting in Europe, Asia, and Australia has never seen many acrocerids in one place.

Some acrocerids with long proboscis (e.g. *Panops* and *Leucopisina*) may be collected on *Leptospermum* flowers. Others with very short proboscis (e.g. *Oncodes*) may be collected on the leaves. Some of them hover in sunshine in clearings.

Eggs.—The eggs may be laid singly or many females may join in mass oviposition on small branches of plants. Each female can produce 1000-4000 very small black eggs. The eggs are usually laid on the underside of branches: they are pear-shaped and are fixed to the plants at the smaller end.

Larvae.—The 1st instar is quite different from the other stages, being very mobile. Acrocerids have trimorphic larvae like the Bombyliidae: 1st stage is apneustic, the 2nd metapneustic, and the 3rd amphipneustic.

The young larva hatches only after many weeks of development: it is elongate, worm-like, and 12-segmented; upperside convex, underside flat. It is ornamented with bristles or scales, and armed with chitinous hooks, which can perforate the chorion of spider eggs or the abdominal integument of the adult spiders. The shape of the mouthparts is very like those of bombyliid or nemestrinid larvae. The last segment of the larva has a disc which enables it to stand vertically or to spring.

The newly hatched larva attacks anything visiting the leaves or branch on which it is, but it dies if the visitor is not a spider. If it be a spider, the larva penetrates into its body through the spiracles or by destroying the articulatory membrane. Little by little the larva consumes all the tissues of the host, leaving the most vital until the end. After preparation of an exit from the body of the host, the larva transforms into a pupa. Some larvae attack spider egg capsules. The larva winters in the body of the host or in the egg capsule, transforming into a pupa in the spring.

Pupae.—The pupae are bare, short, with enormously developed thorax (gibbous). They have 1 pair of spiracles on the thorax and 6 pairs on the abdomen. The emergence of the adult is initiated by a median splitting of the pupal integument.

Number of species.—Acroceridae, according to the review of Sack (1936) were represented at that time by 27 genera and about 175 species: in the Palearctic region, according to Sack, there were 10 genera with 40 species. About half of all known forms were recorded from America and the majority of them from South America. The fauna of Australia, with its four genera, is comparatively poor, the subfamily Philopotinae being quite absent. The poverty of the Australian fauna is difficult to explain. The family is quite old and would be expected to have many representatives in this region, as do Apimaculidae, Theromyzidae, Bombyliidae, etc. but its paucity of species is apparently real. Szalay (1951) estimated that about 250 species were known throughout the world.

KEY TO AUSTRALIAN GENERA OF ACROKERIDAE

1. Antennae long, at least as long as head, without terminal style, inserted near ocelli 2
 Antennae long, without terminal style, attenuated in apical half, inserted at middle height
 of head (New Zealand genus, not yet recorded in Australia) *Apsona* Westw.*
 Antenna short, with terminal style, and inserted near mouth cavity 3
2. Abdomen constricted at 2nd and 3rd segments into hour-glass form. Strongly resembling
 wasps *Leucopsina* Westw.
 Shape of abdomen normal, broad at base, not resembling wasps. *Panops* Lam.
3. Eyes bare. Venation evanescent, some veins quite absent, some very weak. . *Oncodes* Latr.
 Eyes haired. Venation normal, with all veins equally developed *Pterodontia* Gray

Genus LEUCOPSINA Westwood

Leucopsina Westwood, 1876, Trans. Ent. Soc. Lond. 1876: 510.

Belongs to the group of genera with antennae at least as long as head, without terminal style, and inserted near ocelli. Eyes bare. Proboscis of medium size, directed backwards towards the apex of abdomen. Three ocelli. Thorax convex, oval, with strong humeral calli. Closely related to the genus *Panops*, with very similar venation, but distinguished from it very readily by the wasp-like abdomen strongly narrowed at base.

Generotype *L. odyneroideis* Westwood.

LEUCOPSINA ODYNEROIDES Westwood

Leucopsina odyneroideis Westwood, 1876, Trans. Ent. Soc. Lond. 1876: 510, pl. 5, fig. 3.

Brunetti (1926) having seen the type in the British Museum, gave an additional description. The type was collected from New South Wales; sex recorded as indeterminate. The author has seen some specimens of this species and can expand the description and indicate some inaccuracies in the illustrations of Westwood.

Male. -Body black, with bright lemon-yellow spots situated as follows: (1) humeral calli, (2) postalar calli (which can only be positionally so called, as they are not homologous with these calli), (3) narrow fascia along the hind margin of 1st tergite, (4) small lateral spots on hind margin of 2nd tergite, (5) narrow but very clearly demarcated fascia along the hind margin of 3rd tergite, (6) similar fasciae on the hind margin of 2nd and 3rd sternites. Whole body is covered with whitish, extremely small hairs, which can be seen only with magnification; they do not camouflage the ground colour of the body.

Basal 2 joints of antennae, apical portion of proboscis, all tibiae and tarsi, apices of all femora, and genitalia: reddish. Antennae as in *Panops*: basal 2 joints extremely small, like a convex lens, broader than long, 3rd joint extremely long, at least as long as vertical diameter of head, without style, rounded at apex. Proboscis very long, about twice as long as the vertical diameter of the head. Palpi reduced, very short. Face in profile with 2 tubercles.

Hairs on mesonotum yellowish. Wings nearly hyaline, but in the anterior half darkened from the base to the apex along the common stem of the veins r_1 and r_2 and further along r_3 to the apex. Along the cubital vein there is also a dark stripe, but the boundary is very ill defined. Alula nearly absent. Anal cell closed. Five

* See Paramonov (1955).

posterior cells, the 4th is rather long petiolate, the others broadly opened. Vein r_4 with a short recurrent veinlet in basal section. There are 2 $r-m$ veins: one (usual) at base of discal cell, another (unusual) beyond the apex of this cell, connecting m_1 with r_5 a little beyond the bifurcation of r_4 and r_5 . Costal vein yellowish. Halteres brown. Squamae brown, lighter from only the base outwards, densely covered with whitish hairs.

Scutellum, like the mesonotum and abdomen, punctated. Abdomen with strongly narrowed 2nd and 3rd segments. This peculiar shape, with the disposition of yellow spots and stripes, creates a very close resemblance to the genus *Odynerus* (Eumenidae) and this influenced Westwood in the choice of a trivial name.

Length of body 10 mm, of wing 8.5 mm.

Specimens examined.—NEW SOUTH WALES: Milton, 20 miles S. of, 30.ix.1952, S. J. Paramonov, 1 ♂. Bateman's Bay, 4 miles N. of, 22.x.1952, S. J. Paramonov, 1 ♂ (both specimens on flowers of *Leptospermum* sp.); Monga, near Braidwood, 25.xi.1954, I. F. B. Common, 1 ♂; N.S.W., 1 ♂. VICTORIA: Montrose, 2.xii.1945, A. N. Burns, 1 ♂.

The specimens in the author's hands differ from *L. odyneroides* in the following characters: (1) 3rd antennal joint is slightly thickened towards the apex, where it is rounded (in *L. odyneroides* it is "elongato subelavatum", i.e. slightly swollen in the apical half, but with rather acute apex); (2) 2nd antennal joint is a little longer than the very flattened 1st one (in *L. odyneroides* the 1st one is longer); (3) eyes are separated by frontal stripe about as broad as half of ocellar triangle (in *L. odyneroides* they are contiguous); (4) frons is triangular, about as big as ocellar triangle (in Fig. 3a of Westwood the frons is absent); (5) mesonotum quite unicolorous, without longitudinal stripes or crossbands (in Fig. 3 of Westwood there are 2 submedian narrow dark longitudinal stripes, and in front of scutellum there is a crossband); (6) 1st posterior cell (its basal part between the vein $r-m$ and additional crossvein) is distinctly longer than discal cell, twice as long as additional crossvein (in *L. odyneroides* this distance is much shorter); (7) 4th posterior cell has a long petiole (in Fig. 3c of Westwood it is very short); (8) uniform dark brown colouring of wing reaches the apex (in Fig. 3 of Westwood the dark colouring is distinctly narrower and does not reach the apex of wing); (9) base of abdomen has the quite symmetrical form of an hour-glass (in *L. odyneroides* the basal part of this hour-glass is nearly parallel-sided).

Some specimens have quite reddish antennae and legs, whereas the typical form has black femora and black 3rd antennal joint: the specimens with reddish legs are represented by very old material and the author is not sure that the reddish colour is natural, but the result of aging.

This species seems to be a spring form flying mostly in September, October, and November.

Genus PANOPS Lamarck

Panops Lamarck, 1804, Ann. Mus. Hist. Nat. 3: 263.

Epicerina Macquart, 1850, Dipt. Exot. Suppl. 4. p. 97.

Eyes bare. Antennae situated close to the ocelli, long, without a terminal style, longer or slightly shorter than vertical diameter of eye. Proboscis very long, directed backwards to the apex of abdomen. Venation strong. Five

posterior cells, the 4th closed. Vein *r-m* exactly at end of discal cell or even more distal. Vein *r*₄ very often with an additional veinlet directed towards the base of wing. Abdomen large, bladder-like, longer and broader than thorax.

Genotype *P. baudini* Lamarek.

The genus *Epicerina*, with typical species *E. nigricornis*, was described by Macquart (1850). Brunetti (1926) wrote:

"The type of this species (*E. nigricornis* Macq.), recorded from Tasmania and as being in the Paris Museum, was considered lost, but an unnamed specimen found by me in the collection appears to be the missing genotype. It bears a red label (representing the Australian Region), and a register number which Mr. E. Séguy kindly informed me means that it was collected by M. J. Verreaux in Tasmania in 1847. It agrees well with Macquart's description and figures of full insect and head in profile, with one serious discrepancy. Macquart states and figures the proboscis as very short, whereas it is long enough to reach under the belly to the tip of the thorax. Premising this serious oversight (because, as a matter of fact, it is easy to overlook the proboscis when it is closely pressed to the underside of the body), there is nothing to prevent its identity with *nigricornis*. The venation agrees exactly, the black abdomen with blue reflections is characteristic, the tibiae though streaked with black (described as yellow) have the outer side yellowish in the middle pair and the hinder side yellowish in a hind pair. The alleged whitish dust on the abdominal incisions is accounted for by a little short whitish pubescence towards the sides at the bases of several of the segments. The frons is a very small triangle just below the inner upper corners of the eyes. Macquart's expression of it being in the male a "linear point between two triangles" is difficult to explain.

Taking all the points into consideration, the specimen in question is very probably the type."

Thus the basic character of the genus—a short proboscis—was based on a mistake of Macquart. It is highly probable that this genus is only a synonym of *Mesophysa*, which was described by Macquart in 1838. We can, however, safely regard the genus *Mesophysa* as only a synonym of *Panops*.

KEY TO THE AUSTRALIAN SPECIES OF THE GENUS PANOPS

1. Humeral calli black. Abdomen regularly rounded *P. baudini* Lam., ♂, ♀
 Humeral calli yellow. Abdomen with strongly incised inflated segments 2
2. Length of body 18 mm. Mesonotum brownish orange, with 3 broad black stripes
 *P. conspicuus* (Brun.) (sex?)
 Length of body 13–14 mm at most. Mesonotum uniformly dark *P. flavipes* Latr., ♂, ♀

PANOPS BAUDINI Lamarek, ♂, ♀

Panops baudini Lamarek, 1804, Ann. Mus. Hist. Nat. **3**: 265, tab. 22, figs. 3a–d.

Mesophysa marginata Macquart, 1838, Dipt. Exot. **1** (2): 168.

Epicerina nigricornis Macquart, 1850, Dipt. Exot. Suppl. **4**. p. 98, tab. 9, fig. 8.

Mesophysa australasiae Thomson, 1868, Eugenes Resa, Dipt. **1868**: 475 (type seen).

Panops lamarekanus Westwood, 1876, Trans. Ent. Soc. Lond. **1876**: 508, pl. 5, fig. 1.

Ground colour of body black, but the sides of tergites purplish red, not bright; the spots in different specimens developed to a varying extent. Tibiae, tarsi, and apices of femora yellow. Squamae white, with dense, long, erect, whitish hairs.

Occiput, thorax, and scutellum covered with dense, erect, whitish hairs, the length of which on the humeral calli is much greater than the length of 2 basal antennal joints combined. Abdomen covered with similar hairs, which are generally

much shorter, though slightly longer at the sides. Surface of tergites finely punctured, not as coarsely as in *P. flavipes*. Antennae black or dark brown, narrowing at apex, about as long as vertical diameter of eye.

Wings hyaline, greyish. Vein $r-m$ nearly exactly at end of discal cell. Distance between r_5 and r_4 is distinctly broader than between r_1 and r_{2+3} . Length of last portion of m_1 is half the length of r_5 (in *P. flavipes* it is longer than half the length of r_5).

Abdomen inflated, egg-like, underside purplish.

Length of body 11–13 mm, of wing 8–10 mm.

Specimens examined.—NEW SOUTH WALES: Sydney; Upper Hunter R.; Bondi, 19.x.1924, 1 ♂. QUEENSLAND: Gayndah.

This species is easily distinguishable from *P. flavipes* by the short, egg-like abdomen and rather different wing venation, especially in the apical part of wing. The other differences are seen in the following comparison of characters:

<i>P. baudini</i>	<i>P. flavipes</i>
Wings nearly hyaline, slightly yellowish, but very uniformly so	Wings distinctly darkened along anterior margin for approximately half the width of the wing
Abdomen almost egg-shaped	Abdomen elongated
Tergites in profile forming one regularly curved line	Tergites extremely swollen, making dorsal profile wave-like
Abdomen with slightly translucent reddish colour at sides	Abdomen uniformly black
Hairs on 5th tergite same as on others	Fifth tergite with dense yellow golden hairs
Base of r_{4+5} at apex of discal cell	Base of r_{4+5} situated far from the apex of discal cell
The cell above the discal cell at apex is converging	The cell above the discal cell is parallel-sided
Humeral calli black	Humeral calli yellow
Underside of abdomen reddish	Underside of abdomen black

Antennae in females of both species are shorter than in males.

Brunetti (1926) gives some interesting data about the type of *M. marginata* which is preserved in the Paris Museum under this name.

PANOPS FLAVIPES Latreille, ♂, ♀

Panops flavipes Latreille, 1811, Eneyel. Méthod. 8: 710.

Panops flavipes, Wiedemann, 1830, Aussereurop. zweifl. Ins. 2: 649.

Mesophysa scapularis Macquart, 1838, Dipt. Exot. 1 (2): 167.

Wiedemann gave a German rendering of Latreille's description of this species from New Holland and preserved in the Paris Museum. From his description it is evident that the type specimen of Latreille differed in the following respects from the species as generally accepted: (1) scutellum is golden yellowish (as a rule it is dark, with coppery shine, only sides yellowish), and (2) mesonotum with 3 impressed lines (these are usually only marks), but probably our common species is that of Latreille. Brunetti (1926) gave a full redescription of *M. scapularis*.

Ground colour of body black, but 2 basal antennal joints reddish, humeral calli, sometimes a spot high on mesopleurae, and postalar calli bright yellow; sides of scutellum paler yellow; also all tibiae, tarsi, and apices of femora are yellow. Squamae dirty yellowish, but a stripe along the margin is brownish.

Antennae slightly longer than vertical diameter of eye, 3rd antennal joint very gradually broadening towards the apex where it is rounded. Mesonotum, scutellum, and abdomen distinctly punctured (more roughly than in *P. baudini*).

Wings hyaline, but anterior half strongly brown coloured, the posterior edge of this coloured area is ill defined. Vein *r-m* situated very far distal of the apex of discal cell and distal from bifurcation of r_4 and r_5 (in *P. baudini* basad from bifurcation).

Abdomen has a very characteristic shape, the tergites are strongly swollen, especially along posterior portion, and therefore each appears humpbacked. In profile the boundary between them is very deeply sunk, also viewed from above the tergites are deeply separated from one another. Fifth tergite covered very densely with yellow hairs which are all depressed. The hairs on the body are not long and dense, those of humeral calli distinctly shorter than the combined length of the 2 basal antennal joints. Abdomen in female is broader than in male, and broadens distinctly at apex.

Length of body 12.5 mm, of wing 10 mm.

Specimens examined.—AUSTRALIAN CAPITAL TERRITORY: Bendora, Bull's Head, Mt. Franklin, Jan.–Feb., 1948–1952, S. J. Paramonov, 17 ♂♂, 3 ♀♀, all localities above 4000 ft; Bendora, 2 miles S. of, 4.ii.1953, I. F. B. Common, 1 ♂; Bendora, 24.i.1950, E. F. Riek, 1 ♀; Bull's Head, 3 miles S. of, 14.ii.1952, I. F. B. Common, 1 ♀. NEW SOUTH WALES: Moruya, 16.x.1904, 1 ♂; Woolwich, 11.xi.1929, Wassell, 1 ♂; Sutherland, Nov. 1915, E. H. Zeck, 1 ♂; Hawkesbury R., 30.x.1930, A. N. Burns, 1 ♂; Palm Beach, 5.x.1927, 1 ♂; Gundamain (nr. Sydney), 3.x.1926, Boyd, 1 ♂; Mt. Keira, via Wollongong, 14.iii.1948, D. A. Walsh, 1 ♂; Lane Cove, 10.x.1948, N. W. Rodd, 1 ♀; Leota Vale, Hawkesbury R., 16.x.1925, Mackerras, 1 ♀; Gordon (nr. Sydney), 15.xi.1925, Harrison, 1 ♀; Galson, 29.x.1933, H. Willings, 1 ♀; Bowral, Feb. 1923, 1 ♀; Turramurra (nr. Graham), Oct. 1924, 1 ♀; Mosman, 30.xi.1919, G. Don, 1 ♀. VICTORIA: Mt. Wilson, 4.i.1931, A. N. Burns, 1 ♂; Flowerdale, 15.xii.1954, A. Neboiss, 1 ♀.

The determination of sex in this genus, as in other genera of *Acroceridae*, is difficult; Brunetti, for example, could not separate them. The genitalia are of a similar structure, with lobes in the female similar to forceps.

Female genitalia can be recognized by the presence of 2 broad lobes forming an arc and nearly touching one another; in male there are 2 forceps which touch one another, but they are acute and never form an arc.

The examination of specimens from different localities has shown great variability in this species.

Length of the antennae can be equal to, or distinctly shorter than, vertical diameter of the eyes. Third antennal joint may be broader in its apical half than in its basal half, or broader at the middle, attenuating towards the apex and base.

Head in the area of antennae may protrude distinctly upwards, the antennae appearing to be sitting on the poorly developed tubercle, or head may have usual regular form, not protruding upwards, not appearing to form a poorly developed tubercle.

Upper part of occiput may have a distinct bluish green shine, or be only black.

Hairs on mesonotum may be dense, and longer than the combined length of the 2 basal joints of the antennae, or they may be only as long as one of the basal antennal joints.

Dark colour of wing may not be intense, diffused at apex of submarginal cell, and lower basal cell dark only along the veins, or the dark colour of the wing stronger, and more regular, lower basal cell dark.

Hairs on tergites may be about as long as on mesonotum, almost as long on 1st to 5th tergites, or hairs on tergites extremely short, shorter than on mesonotum, distinctly denser and longer over the 5th tergite.

The specimens from different localities have all combinations of the above-mentioned characters, therefore the author regards them as belonging to one very variable species.

PANOPS FLAVIPES var. BURNSI, var. nov.

Among some dozens of specimens of *P. flavipes* the author has found one differing from the remainder in possessing yellow spots on postalar calli, a very narrow yellow hind crossband on 1st tergite, 2 lateral triangular spots on the 2nd, and a rather broad crossband at the hind margin of the 3rd tergite. Unfortunately the specimen is headless and damaged; it was collected by Mr. A. N. Burns on 28.xi.1931 at Ferntree Gully, Vic. Probably it represents a new species, but the author prefers to regard it as var. *burnsi*, var. nov. The type of the new variety is in the private collection of Mr. A. N. Burns.

PANOPS CONSPICUUS (Brunetti)

Epicerina conspicua Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 17: 579.

This species is unknown to the author. Type from Kalamunda, W.A., in the British Museum.

Genus PTERODONTIA Gray

Pterodontia Gray, in Griffith, 1832, Animal Kingdom 15 (34): 779, pl. 128, fig. 3.

Nothra Westwood, 1876, Trans. Ent. Soc. Lond. 1876: 514 (?).

Head extremely small, nearly completely occupied by the eyes which are contiguous in both sexes. Three ocelli. Viewing the insect from above the head seems to be absent.

Eyes with dense and long hairs. Antennae very small, hidden on underside of head, with a terminal "style" consisting merely of 2-3 bristles, which are situated very closely together.

Mouth-opening more or less concealed. Proboscis short.

Abdomen extremely broad, inflated. Wing hyaline. Venation strong, but very peculiar. Vein *r-m* absent. All 3 radials simple, without bifurcation. Two posterior cells. Anal cell closed. One submarginal cell. A great sexual dimorphism in shape of wings: those of the female have the usual shape, in the male the costa has in its apical part a strong tubercle, and wing appears as if broken. A short but acute spine is always present at this tubercle.

Generotype *P. flavipes* Macquart, from America.

The type of *Nothra bicolor* Westw. was examined by the author; as usual, all *Pterodontia* are males and all *Nothra* are females.

Only one species, *P. melli* Erichs., was present in Australia. The species was described by Macquart (1838) as *P. flavipes*, but this name was preoccupied and Westwood (1848) proposed a new name—*P. macquarti*; however, Erichson (1840) had described this species under the name *P. melli* and this name has priority over the name of Westwood.

White (1914) described a second species from Tasmania, *P. variegata*, but it is very possible that it is only a synonym of *P. melli*. The author, however, considers it necessary to mention White's description of *P. variegata*, which contains the comparison of characters of both *P. melli* and *P. variegata*.

PTERODONTIA MELLI Erichson

Pterodontia flavipes Macquart (nec Gray), 1838, Dipt. Exot. **1** (2): 175; 1840, op. cit. **2** (1): pl. 1, fig. 2; 1843, op. cit. **2** (3): pl. 34, fig. 3 (name preoccupied by Gray for American species in 1832).

Pterodontia melli Erichson, 1840, Entomographia **1**: 163 (collector Mell, therefore *melli*, but not *mellii*).

Pterodontia macquarti Westwood, 1848, Trans. Ent. Soc. Lond. **1848**: 97 (renamed but *P. melli* has priority).

Nothra bicolor Westwood, 1876, Trans. Ent. Soc. Lond. **1876**: 514–15, pl. 6, fig. 4 (*Nothra* is the female sex of *Pterodontia*).

Macquart (1838*b*, pl. 21, figs. 5a and 5b) figured a wing and head of *P. flavipes* but while the wing is of this genus, though very incorrectly drawn, the head is that of an acalyptrate muscid, and he acknowledges this error later (1840, pl. 1, fig. 2) where he gives a correct diagram of the wing, and states that the acalyptrate previously figured is *Trigonosma perilampriformis*.

Male.—Body black. Antennae, fore legs and tarsi, scutellum, postalar calli, and sides of 2nd, 3rd, and 4th tergites yellow. Hairs on whole body black. Black median stripe on abdomen is narrowing to the apex. Costa quite extraordinary: in area of apices of r_1 and r_{2+3} costa is humped, with an additional acute tubercle.

Female.—Body and antennae yellow, but head black, mesonotum on disc black, but sides broadly yellow, underside of thorax in coxal areas slightly darkened; on tergites dark, median irregular spots not touching the hind margin. All hairs and veins of wing yellow. The black spot on mesonotum at anterior margin parallel-sided, as broad as distance between humeral calli, then suddenly broadening and occupying all disc, stopping at postalar calli. In front of scutellum there is also a yellow spot.

Shape of wing quite normal. Female with usual form of wing, described as the genus *Nothra*.

Length of body 8.5 mm, of wing 7.5 mm.

This species may be Australia-wide in distribution, but the author knows it only from Victoria, New South Wales, and Queensland.

Specimens examined.—AUSTRALIAN CAPITAL TERRITORY: Black Mountain, 20.ii.1934, F. J. Gay, 1 ♂. NEW SOUTH WALES: Merimbula, 14.ii.1950, F. E. Wilson, 1 ♂; Eungai, J. Armstrong, 1 ♂. VICTORIA: Blackwood, V. Miller, 1 ♀. QUEENSLAND: Bundaberg, 1916, H. Brown, 1 ♂ (W. W. Froggatt Collection).

PTERODONTIA VARIEGATA White

Pterodontia variegata White, 1914, Pap. Roy. Soc. Tasm. 1914: 68, fig. 10.

White distinguished this species from *P. melli* as follows:

"The only other known Australian species of *Pterodontia*, *P. macquartii* is described as being black, with the scutellum and sides of abdomen red; legs yellow; anterior femora black. The colouring of the legs will therefore at once distinguish *P. variegata*, which has the anterior femora yellow, the middle and posterior femora black, and middle and posterior tibiae brown."

Type ♂, described from Lefroy, Tas.

PTERODONTIA DAVISI, sp. nov.

Much smaller than *P. melli*. Head, thorax, and scutellum black, only postalar calli dark brown. Abdomen uniformly dark brown. All hairs black, except on legs. Lower calypter brownish, with black hairs. Halteres brown. Wings hyaline, of usual form, slightly protruding near the end of r_1 , but not so strongly as in *P. melli*; the spines absent, only the apical portion of r_1 is very swollen. Legs yellow, tibiae and tarsi whitish, hairs whitish. On dorsal side of all tibiae there are dense and long hairs, longer than the diameter of the tibiae, and erect, not declined as in *P. melli*. The middle longitudinal depression on mesonotum, which is present in both sexes in *P. melli*, absent.

Type specimen is undamaged, but slightly deformed, possibly not completely hardened before collection.

Length of body 5 mm, of wing 5 mm.

Specimens examined.—NEW SOUTH WALES: Austinmer, Feb. 1928, H. C. Davis, 1 ♀.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Genus ONCODES Latreille

Ogcodes * Latreille, 1796, Préc. Car. Gen. Ins. p. 154.

The first *Oncodes* species from Australia was described by Walker in 1852 (*basalis*). In 1876 Westwood added four species (*fortnumi*, *tasmanicus*, *ignavus*, and *darwinii*). In 1906 Wandolleck added *doddi*, and in 1907 Froggatt gave a very insufficient description of *Acrodes* (sic) (= *Oncodes fumatus*).

In 1914 White described four species from Tasmania (*flavescens*, *nigrinervis*, *ater*, and *pygmaeus*) overlooking the work of Westwood and erroneously considering that he was the first dipterist to describe species of *Oncodes* from Tasmania, although Westwood named one of his species *O. tasmanicus*. In 1926 Brunetti described four new species (*variegatus*, *insignis*, *castaneus*, and *victoriensis*), probably also overlooking the work of Westwood, because in comparing the new species with *basalis* Brunetti said nothing about Westwood's species. Hardy (1916, 1918, 1922, and 1940), quite wrongly regarded all these 15 species as only colour varieties of *basalis*.

* The author prefers to use the more correct form *Oncodes* instead of *Ogcodes*, and this emendation is used by many authors not only in this case but in others such as *Oncodocera* (Bombyliidae). This correction has been accepted by all catalogues, and there is no reason to return to Latreille's incorrect orthography.

Head of the male larger than that of the female, almost all occupied by the eyes except for the small vertex, on which are 2 ocelli and the small space at the bottom of the head on which are the antennae and the indistinct mouthparts; frons slightly produced below the point where the eyes touch; back of the head rather inflated in the male, but more so in the female, and adpressed to the thorax; jowls slightly inflated. Proboscis absent, the site being closed with a membrane. Eyes enormous, quite bare. Antennae apparently 2 jointed, placed on the extreme lower part of the head, apparent basal joint cylindrical, short, and thick; apparent 2nd joint oval, with a long thin apical style which is dilated at its base but ends in a minute hair-like bristle.

Thorax forming a complete sphere; humeral, pre-alar, and postalar calli large, but not very conspicuous; pubescence rather dense and soft, but hardly abundant enough to be furry and without the slightest sign of bristles or long hairs even on the postalar call or the margin of the scutellum. Scutellum large, with a very deep, rounded margin which leaves only a small portion of the disc rather flat, pubescence similar to that on the thorax; metanotum rather small.

Abdomen dorsally arched but hardly globular, short ovate with a blunt base and tip in the male, but short and round in the female, with 5 obvious segments; pubescence fairly abundant. Genitalia concealed beneath the rather small 5th segment.

Legs rather short and stout, but simple and without any trace of spurs or processes; tarsi with the 1st and 5th joints longer than the others. Pulvilli and claws well separated from the 5th tarsal joint; claws long and thin; pulvilli in the male almost equally long and thin, but shorter and more pad like in the female.

Wings short in the male, but larger and longer in the female; venation very imperfect. The wing tip is clear of all venation over a very large area; radial vein quite absent; cubital vein sloping downwards, incomplete, and not forked; discal vein indicated by 3 incomplete veins running towards the wing margin far behind the wing tip. Squamae (thoracic) enormous, depressed, and clothed all over their upper surface with rather sparse woolly pubescence; alar squamae rather small but thick, clothed with only minute down. Halteres on comparatively short stems, hidden beneath the thoracic squamae.

Sexual dimorphism is very great in regard to the colour of the abdomen, and it is quite evident that the different sexes of some species have been given different names.

As a rule the female abdomen is more extensively coloured, is darker, having broad black fasciae and lighter hind margins to the segments or wholly black or dark, never having a median row of more or less rounded markings, which is typical in the males.

Brumetti (1926) also virtually failed to give the characters for separating species: in his key to identification he uses terms such as "conspicuously characteristic species", alternative to "less conspicuous species" etc. He also failed to state the sex of specimens.

Genitalia of both sexes are easily confused, but if examined from the ventral side they are easy to separate: in the male the hind margin of the 5th sternite touches

the genitalia which consists of 1 dentate genital plate, penis, and 2 spoon-like lobes. In the female the hind margin of 5th (or actually 6th) tergite touches a very swollen lobe embracing the genitalia which consists of 2 spoon-like lobes; these lobes are haired in both sexes. The difficulty is that genitalia, usually curved downwards to the tergites and the distal parts of abdomen, are hidden. The female abdomen is distinctly broader and is also of help in identification.

KEY TO AUSTRALIAN SPECIES OF THE GENUS *ONCODES*

1. Lower basal cell (*M*) separated from posterior cell by pale but quite distinct vein; sometimes this vein can only be seen if the wing is examined obliquely 2
Lower basal cell united with the last posterior cell, no trace of a vein separating them 10
2. Whole body black, shining, only tibiae and tarsi yellow. Wings quite hyaline. Tas., Vic.*O. aler* White, ♂, ♀
Abdomen always lighter than thorax; thorax black, abdomen dark brown; if some parts of abdomen black (rarely), the hind margins of tergites brownish or reddish yellow ...3
3. Femora only slightly swollen; at broadest point they are only a little broader than the tibiae, which are cylindrical. Sides of abdomen with depressed hairs towards the middle. N.S.W.*O. tenuipes*, sp. nov., ♂
Femora distinctly swollen, comparatively thick, distinctly broader than tibiae. Tibiae mostly much broader at apices than at bases 4
4. Legs (especially femora) predominantly black 5
Legs predominantly yellow or reddish yellow 7
5. Veins of wing dark and prominently marked. Abdomen black, with hind margins of segments white. Female unknown. Tas.*O. nigritervis* White, ♂
Veins of wing faint, yellowish. Abdomen black, with hind margins of tergites yellow, these fasciae are broader at sides 6
6. Hairs on mesonotum very short, about as long as diameter of the anterior spiracle dark. Sides of 2nd-5th tergites with bright yellow triangular spots jointed by some narrow fasciae on hind margin. Femora at apices yellow above. Mt. Kosciusko, N.S.W.*O. glomeratus*, sp. nov., ♂
Hairs on mesonotum very long, about as long as one-third of anterior diameter of head, light yellow markings of abdomen much narrower and not so bright. Legs black. Mt. Kosciusko, N.S.W.*O. lucidus*, sp. nov., ♂
- 7.* Frons with small but distinct bunch of hairs. N.S.W., Tas., Vic.*O. luteifrons*, sp. nov., ♂
Frons bare, or with microscopic pale hairs 8
8. Sides of thorax and abdomen predominantly yellow (red-orange) sides of mesonotum, humeral and postalar calli also yellow. Wings yellowish. N.S.W.*O. canberranus*, sp. nov., ♂
Abdomen predominantly dark, mesonotum always dark 9
9. Abdomen in both sexes with distinct whitish or yellowish lines (except on the tergites). Larger species (see description)*O. fortisui* Westw., ♂, ♀
Abdomen in both sexes without markings on abdomen, or these markings are very reduced. Smaller species. Tas., N.S.W. (see description)*O. pygmaeus* White, ♂, ♀
10. Scutellum completely or predominantly yellow, or at least one-third of scutellum yellow 11
Scutellum completely black 13
11. Scutellum completely yellow. Large species. Male unknown. N.S.W.*O. armstrongi*, sp. nov., ♀
Scutellum partly black. Small species 12

* All species from point 7 of the key have the antennae (especially the 3rd segment) shorter than the thorax.

12. Disc of scutellum yellow, marginal area black. Tergites with very broad black fasciae. Qld. *O. pusillus*, sp. nov., ♂
Scutellum black, but more than the middle third (longitudinally) orange. On each segment of abdomen a black transverse band, broadest in middle, narrowing towards sides, where it is almost interrupted and widened again into a good-sized, squarish spot on each side margin. Qld. Sex unknown *O. variegatus* Brun. 14
13. Legs deep black, including tarsi; only basal halves of all tibiae yellow. Black and yellow areas strongly contrasting 14
Legs with another pattern 16
14. Tips of fore coxae narrowly yellow. S.W. Aust. *O. insignis* Brun., ♂
All coxae deep black 15
15. Dark fasciae on tergites broadly reach the sides of tergites. W.A. .. *O. wilsoni*, sp. nov., ♂
Dark fasciae on tergites not reaching the sides of tergites (except in one specimen, in which, however, the mesopleurae have a yellow spot, whereas in *O. wilsoni* they are black, and without a spot). Qld. *O. deserticola*, sp. nov., ♂
16. Wing entirely blackened, being slightly lighter towards hind margin, but the marginal area itself is distinctly dark (under magnification the colour of wing is brownish, not yellow) *O. waterhousei*, sp. nov., ♀
Wing hyaline or only darkened at basal half or slightly yellowish on whole surface 17
17. Males (as well as from the genitalia, they can be recognized by the pattern of the abdomen; in males 2nd and 3rd tergites always reddish brown, not black; in females, on these tergites there are always black fasciae)* 18
Females 20
18. Species 8-9 mm in length *O. darwini* Westw., ♂
Species under 8 mm in length 19
19. *O. basalis* (Walk.), the commonest Australian species, and *O. doddi* Wandolleck, a doubtful species (see description)
20. Species 8-10 mm in length *O. darwini* Westw., ♀
Species under 8 mm in length 21
21. *O. basalis* (Walk.) and *O. castaneus* Brun., a doubtful, poorly known species (see description)

ONCODES BASALIS (Walker)

Henops basalis Walker, 1856, *Insecta Saundersiana*, Dipt. 1: 203.

Brunetti (1926) has added some interesting information about this species:

"The type in the British Museum, from New South Wales (ex Saunder's Coll.), is in good condition and bears a striking resemblance to my *rufomarginatus* from Ceylon, the difference being as follows:

Hind corners of thorax and the scutellum wholly black; hind tibiae all orange; second abdominal segment (the first being extremely short and easily overlooked) all black, except the conspicuous whitish hind margin; ground-colour of rest of abdomen brownish yellow; third segment with a very large median black spot extending over the white hind margin; fourth segment with a similar black spot not encroaching on hind margin; fifth and sixth segments without black markings in median line.

Length nearly 5 mm.

In *rufomarginatus* the black median spots occur on all the segments and are more strictly transverse bands extending across more than half the width of the segment. In *basalis* the black colour in the anterior femora only covers the basal half and on the hind legs reaches a little further,

* Among material available to the author are some males from Chatswood, N.S.W. with the typical abdominal pattern of females. Unfortunately none of the specimens is well enough preserved for description.

the colour in all the legs ending abruptly. In *basalis* the black extends beyond the middle in the anterior legs and to still further in the hind pair, and ends on all legs indistinctly."

It will be useful to quote a letter of July 22, 1955, in which Mr. H. Oldroyd, British Museum, kindly informed the author:

"We have been able to find only one type of *Oncodes* described by White, that of *O. flavescens*. The vein between the lower basal cell and the last posterior one is present in this type, but is absent, as you suggest, in *O. basalis* Walker.

We have the types of four Australian species of Brunetti: *insignis*, *variegatus*, *castaneus* and *victoriensis*, all with the vein absent."

The difference between *basalis* and *darwini* are not quite evident to the author. Generally speaking, greater size is the only distinguishing character of *darwini*. Only the study of a series of specimens of both sexes from the same locality can solve this problem. Unfortunately the author has seen only series of one sex.

It seems that *basalis* is very variable in size and pattern. The material examined by the author exhibited three types of wing coloration: (1) wings nearly hyaline, only darkened along the costa in the basal area; (2) wings distinctly darkened in basal part, but quite hyaline in the apical part; (3) wings regularly smoked on whole surface (mostly in small specimens). Despite all efforts, the author could not find other characters, and accepts all forms as colour variations. However, more and better preserved material may enable the detection of other differences.

Specimens examined.—AUSTRALIAN CAPITAL TERRITORY: Cotter R., 26.x.1930, A. L. Tonnoir, 1 ♂; Black Mountain, 27.x.1936, A. L. Tonnoir, 1 ♂; Canberra, 5.xi.1952, E. F. Riek, 1 ♂; Canberra, 29.xi.1953, M. F. Day, 1 ♂; Canberra, 15.iii.1954, H. M. Cameron, 1 ♂; Canberra, 7.xii.1954, Z. Liepa, 1 ♂; Canberra, 29.xi.1953, 1 ♀; Canberra, 8.ii.1954, K. L. Taylor, 1 ♀. NEW SOUTH WALES: Moree, 20.ii.1910, W. W. F., 1 ♂; Baulkham Hills, 30.ix.1925, G. Wright, 1 ♂; Kurrajong, Oct. 1931, K. K. Spence, 2 ♂♂; Mar. 1933, 1 ♂; Como, 30.x.1943, W. W. Froggatt, 1 ♂; Colo Vale (nr. Mittagong), 19.ii.1954, A. Dyce, Sydney, 1 ♀; Sydney, W. W. F., 1 ♀; Guyra, 21.i.1949, A. Dyce, 1 ♀; Concord, Dec. 1950, A. Dyce, 1 ♀; Bega, 15.iii.1954, 6 ♀♀. VICTORIA: Colac, 9.i.1927, F. E. Wilson, 1 ♂, 12 ♀♀. WESTERN AUSTRALIA: Donnybrook, 9.x.1938, K. R. Norris, 1 ♂, 15 ♀♀.

ONCODES DARWINI Westwood

Oncodes darwini Westwood, 1876, Trans. Ent. Soc. Lond. 1876: 516.

?*Oncodes victoriensis* Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 605.

The type (male) in Department of Entomology, University Museum, Oxford, was examined by the author, thanks to the kind assistance of Professor G. Varley.

The lower basal cell (*M*) is not separated from the last posterior cell; the vein separating these cells, which is present in many species, is here absent. Anal cell is separated behind by a poorly developed but distinguishable vein. Anal cell broadly opened.

Wing quite hyaline, veins yellow at costa, and yellowish on the rest of surface. Crossvein *r-m* very poorly developed, no vein connecting it with other veins of hind half of wing. Squama alaris very large, milky, with a narrow hyaline stripe along the yellow rim; hairs on squama yellowish.

Frons with a deep furrow. Mesonotum and scutellum black, no reddish or yellowish spots or stripes on the thorax. The whitish membrane of sides of thorax is not in consideration. Legs reddish yellow, only basal half of hind femora black.

other femora with less developed black colour. All tarsi blackened, sharply contrasting with yellow colour of tibia. All tibiae, especially the last pair very massive, thickened towards the apex. Hind metatarsus about as long as 3 following joints, slightly shorter.

Hairs on mesonotum yellow, comparatively long and dense.

Abdomen predominantly reddish yellow, nearly transparent, each tergite (except the 1st one) with rather broad whitish hind crossband. Three basal tergites with black diminishing medium spots; the spot on the 4th tergite nearly absent. On 2nd and 3rd tergites the black spots cover the most part of whitish hind margin of tergites. At sides of 1st 4th tergites there are also black spots. Venter yellow.

Length of body in type 9 mm, of wing 7.5 mm; legs in type broken.

The author is not quite sure that this species is a "good" species. Possibly it is only a variation of *basalis*, but represented by large specimens. The author prefers always to separate the forms if there is a doubt, because if in the future it should be found that both forms are conspecific, the geographical, biological, and other data will be combined, but if it is found that one species is in fact represented by two different forms, it would be impossible to state to which species the data applied.

There are some differences between *basalis* and *darwinii*: *darwinii* is much bigger, about twice the size of the other species, but there are all gradations of size between the smallest *darwinii* and the largest *basalis*. Yellow colour of femora of *darwinii* occupying usually the apical half, in *basalis* more than a half. Often the anterior side of fore tibiae in *basalis* is slightly darkened; in *darwinii* it is uniformly yellow. The only difference between females is the larger size of those of *darwinii*.

Specimens examined.—AUSTRALIAN CAPITAL TERRITORY: Canberra, 10.iii.1948, S. J. Paramonov, 1 ♀; Canberra, 22.xi.1950, S. J. Paramonov, 1 ♀; Canberra, 9.iii.1954, A. J. Nicholson, 1 ♀. NEW SOUTH WALES: Acacia Plateau, Bogan R., J. Armstrong, 2 ♂♂; Williams R. (nr. Culkers Pass), 27.x.1926, A. Musgrave and T. G. Campbell, 1 ♂; Bombala, 25.ii.1921, W. W. Froggatt, 1 ♀; Grenfell Rd., 17 miles from Young, 16.x.1950, P. B. Carne, 1 ♀. TASMANIA: Lake St. Clair, 14.i.1937, G. and C. Davis, 1 ♂.

ONCODES VICTORIENSIS Brunetti

Oncodes victoriensis Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 605.

Described by Brunetti from eight specimens sent to him by the National Museum, Melbourne: "Warburton District (type), Frankston, Glenowom (?), all Victoria; Nanaheim, New South Wales." The latter specimen has paler legs and is in bad condition and probably immature, but apparently conspecific. A ninth specimen amongst unnamed material in the British Museum is probably *victoriensis* also, from Townsville, Qld., 14.vi.1901, F. P. Dodd. Examination of the labels shows that Brunetti has wrongly deciphered two of the above localities. They must be "Glenrowan", and "Narrabeen".

Four female paratypes are preserved in the National Museum, Melbourne. Type in the British Museum. Very probably this species is only the female of *darwinii*, but the author considers it wiser to wait for further material.

ONCODES ARMSTRONGI, sp.nov., ♀

Closely related to the *basalis-darwini* group, nearer to *darwini*, from which it does not differ structurally.

As in some specimens of *basalis* or *darwini*, there is, in some specimens, behind the ocellar tubercle, a more or less well-developed additional tubercle; it may be acute, blunt, or otherwise (only 3 specimens), showing all sorts of variability in shape, sometimes higher than ocellar tubercle. However, there are specimens without it.

Humeral calli with broad stripe laterally, postalar calli and scutellum yellow, only disc of mesonotum black; sides of thorax predominantly yellow, only above coxae are there black spots. Wings hyaline, with pale veins.

Legs brownish, upperside of tibiae yellow, apices of femora yellow, tarsi dark brown. Calypters slightly milky, with yellow rim and yellowish erect hairs.

Abdomen black, with hind margin of all tergites narrowly yellowish, underside quite yellowish, hairs very short, yellowish; abdomen is very broad, much broader than thorax.

Length of body 6.5–10 mm, of wing 6–8 mm.

Specimens examined.—NEW SOUTH WALES: Acacia Plateau, Bogan R., J. Armstrong, 3 ♀♀.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra. Male unknown.

ONCODES WATERHOUSEI, sp.nov., ♀

Closely related to *darwini* and *armstrongi* but distinguishable by its darkened wings which are only slightly lighter at hind margin. Veins also brown. Anal cell broadly opened. Humeral and postalar calli yellow. Legs black, only articulations of femora with tibiae are narrowly yellow. Calypter milky, brownish rimmed. Frons protruding, with a deep median furrow.

Length of body 9.5 mm, of wing 8.5 mm.

Specimen examined.—NEW SOUTH WALES: Mossy Point, 23.xii.1952, D. F. Waterhouse, 1 ♀.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra. Male unknown.

ONCODES DODDI Wandolleck, ♂ (?)

Oncodes doddi Wandolleck, 1906, Trans. Ent. Soc. Lond. 1906: 131, figs.

The venation shown in Wandolleck's figure has the following peculiarities: (1) anal vein (a_2) is developed only in its basal half, the apical half being quite obsolete; (2) the vein separating the lower basal cell from the posterior cell is absent; (3) below the bifurcation of the radial stem and m_2 there are no veins or traces of them. From another figure it can be stated that the ocellar triangle is very prominent; the hairs on the mesonotum dense but short and the hind metatarsus (if the figure is exact) only slightly longer than the succeeding tarsal joint.

An uncertain species, the position of which can be clarified only after examination of the type. The type, from north-eastern Australia, is probably in the British Museum. Probably it is only a synonym of *basalis*.

ONCODES INSIGNIS Brunetti

Oncodes insignis Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 601.

Described by Brunetti from a unique male in the British Museum, from Kalamunda, south-western Australia, and collected by Mrs. R. H. Reade. A very striking species by the red abdominal bands and bases of tibiae. There are two forms in the author's hands which are extremely closely related to *insignis* and probably belong to it. However, the variability of *insignis* is quite unknown (only one male is described), the localities are different as well as some characters; therefore, the author thinks it will be wiser not to confuse them, and prefers to describe them as separate species (see *O. wilsoni*, sp. nov., and *O. deserticola*, sp. nov.).

ONCODES WILSONI, sp. nov., ♂

Very closely related to *insignis*, but differs mostly in colour of legs: femora deep black, shining; tarsi black, dull (anterior tarsi with claws a little longer than tibiae); tibiae reddish, but apical half darkened, without a sharp boundary between the two colours, the anterior side of tarsi darkened more than the posterior. Hind metatarsus about as long as combined length of 2 succeeding joints and distinctly shorter than combined length of the 3 succeeding joints.

Frons extremely small, flush, bare. Ocellar triangle low, behind it the occiput is not swollen but regularly descending. Hairs on occiput extremely short, shorter than on mesonotum.

Mesonotum short-haired, the length of hairs at most twice as long as the vertical diameter of the anterior spiracle. Postalar calli reddish yellow from base of wing to the upper corner of scutellum, covered with yellowish hairs over almost the whole surface.

Wings colourless, costa dark brown, radial veins brownish. Vein usually separating lower basal cell from the last posterior cell absent. Anal cell at apex broadly open. Lower calypter transparent, not milky, with brownish rim, a brownish stripe at base.

Abdomen black, shining, the reddish yellow fasciae on posterior of tergites occupying only the last third of the tergites, at sides they have a triangular prolongation into the black colour. Venter yellow, with narrow black basal fasciae.

Length of body 6 mm, of wing 5 mm.

Specimen examined.—WESTERN AUSTRALIA: Bunbury, 6.xi.1949, F. E. Wilson, 1 ♂.

Type in the collection of Mr. F. E. Wilson, Melbourne.

ONCODES DESERTICOLA, sp. nov., ♂

Very closely related to *wilsoni*, only difference in pattern on legs and abdomen and in size.

Tibiae have two contrasting colours: yellow basal and black apical. Abdomen with yellow hind margins on all tergites, including the 1st, and very broad reddish yellow lateral spots on 2nd, 3rd, and 4th tergites (in one specimen the reddish colour is quite reduced in extent and dark).

Length of body 4.5 mm, of wing 3.5 mm.

Specimens examined.—QUEENSLAND: Bransby-Nokandra, 9.xi.1949, S. J. Paramonov, 2 ♂♂ (1 designated type); Burdekin R., 40 miles W. of Collinsville, 15.ix.1950, E. F. Riek, 1 ♂. Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

ONCODES VARIEGATUS Brunetti

Oncodes variegatus Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 594.

Sex unascertainable due to the method of mounting. Described by Brunetti from a unique specimen in the British Museum from Townsville, Qld., 14.vi.1901, F. P. Dodd. A very striking and handsome species.

This species has a considerable resemblance to *basalis*. The latter species differs materially in the all-black thorax and scutellum, the different abdominal markings, although at first sight they appear very similar, the black basal half of all the femora, and, lastly, the narrowly black front margin towards the sides of the sternites.

From Brunetti's key it is evident that the middle third of scutellum (longitudinally) is orange.

ONCODES CASTANEUS Brunetti

Oncodes castaneus Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 605.

Described by Brunetti from one apparent female in the British Museum, from south Queensland, collected by Dr. T. L. Bancroft. It is just possible the type is somewhat immature, in which case the colour of the abdomen and to some extent the legs may be as dark as the thorax in matured specimens. Examination of the type in the British Museum can clarify the true systematic position of this species.

ONCODES PUSILLUS, sp. nov., ♂

In the *basalis* group but the male has broad black fasciae on the abdomen, as in the female of this group.

Head depressed from front. Occiput nearly bare. Humeral calli, a large spot behind and inwards, lateral stripe, postalar calli, and the disc of scutellum yellow. Yellow pattern of mesonotum is similar to that of *armstrongi*, but in the latter species all the space between the humeral calli is black.

Upper part of mesopleurae black, middle part of sides of thorax yellow. Legs predominantly yellow, but tarsi darker, hind femora dark. Calypter brownish, black-rimmed. Wings hyaline, with dark veins. Halteres dark.

Abdomen black above, with narrow yellow hind margins to all tergites; yellow below.

Length of body 4.5 mm, of wing 4 mm.

Specimen examined.—QUEENSLAND: Inkerman, 5.ix.1950, E. F. Riek, 1 ♂.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra. The type appears to be a newly emerged specimen, with crumpled wings and legs.

ONCODES FUMATUS Froggatt

Acrodes fumatus Froggatt, 1907, "Australian Insects", p. 298.

"*Acrodes*" is a misprint for *Oncodes*. This species is a homonym of *Oncodes fumatus* Erichs., 1846, and should be renamed, but it is evident that it is a synonym

of the species described by Walker or Westwood. The location of the type is unknown, and probably it was never designated. On account of this the author regards the redescription of the species as unnecessary. Froggatt wrote:

"*Acrodes fumatus* is a much smaller species, about 1/5 of an inch in length; the head and thorax are black; the bladder shaped abdomen is tawny yellow, with parallel stripes of black down the centre and sides, and transverse white bars at the apex of each segment. They were collected in numbers about Cook's River, near Sydney."

ONCODES FORTNUMI Westwood, ♂, ♀

Oncodes fortnumi Westwood, 1876, Trans. Ent. Soc. Lond. 1876: 516.

Oncodes tasmanica Westwood, 1876, loc. cit.

Oncodes ignava Westwood, 1876, loc. cit.

Oncodes flavescens White, 1914, Pap. Roy. Soc. Tasm. 1914: 70, fig. 11.

Oncodes fratellus Brunetti, 1926, Ann. Mag. Nat. Hist. (9) 18: 604.

The author has examined the types of *fortnumi*, *tasmanica*, and *ignava*, all in the Hope Museum, Oxford. All are males and in imperfect condition. All belong to the group with a vein separating the lower basal cell from the last posterior cell, and are of about the same size, with yellow legs and comparatively long hairs. All have deep black thorax and brown abdomen with a different proportion between brown colour and reddish yellow markings. All have whitish yellow hind margins to the tergites, and the middle part of the 5th tergite bare. The author cannot find any essential differences between them and accepts them as belonging to one species—*fortnumi*.

The abdomen of the type of *fortnumi* is predominantly dark brown, 1st tergite quite dark, 2nd also, with very narrow whitish yellow hind margin and small triangular brownish yellow spots at sides along the hind margin; 3rd tergite is almost completely yellow-brown, darker in basal half and with a narrow whitish hind margin; 4th tergite is similar to the 3rd, but the yellow-brown colour occupies a greater area; 5th tergite is yellow-brown, with darker spots only at sides of fore margin and whitish hind margin; 6th is uniformly yellow-brown.

The abdomen of the type of *ignava* has the same pattern as *fortnumi*; the 6th tergite is dark brown; 5th tergite also dark brown with a triangular yellow marking in the middle in front of the whitish hind margin; 4th tergite is dark brown in basal half, but with distinct incisions at the sides (in *fortnumi* the boundary of the brown colour is quite straight), in apical half the colour is yellow-brown and the hind margin narrowly whitish; 3rd tergite with same pattern as 4th, but the dark brown colour is prolonged triangularly to the hind margin; 2nd is dark brown with exactly the same pattern as in *fortnumi*; 1st tergite dark brown.

The abdomen in *tasmanica* is similar to that of *ignava*, but with more extensive yellow-brown colour of the 5th, 4th, and 3rd tergites, where the dark brown colour is represented only by triangular spots at the sides.

The author has a large series of specimens of *fratellus* (cotypes) which show much individual variation in size and form of abdominal markings; in general, this series is slightly darker than the types of *tasmanica* and *ignava*, but since 1876 the specimens of Westwood have evidently lost the intensity of their natural coloration.

As the author cannot find morphological characters separating these species, he is forced to regard them as synonyms.

The types of *flavescens* (a male from Launceston, Tas.) and *fratellus* (a male from Victoria) which the author thinks are also synonyms of *fortnumi*, were not available for study.

Specimens examined.—AUSTRALIAN CAPITAL TERRITORY: Canberra, 10.xi.1952, K. R. Norris, 1 ♂; Canberra, 17.xi.1954, Z. Liepa, 1 ♂. NEW SOUTH WALES: Beaconsfield, 8.xii.1923, G. F. Hill, 4 ♂♂; National Park, Sydney, 27.ix.1925, 1 ♂; Yass, 28.iii.1930, K. English, 2 ♂♂; Broken Hill, 19.xi.1949, E. F. Riek, 2 ♂♂; Wilcannia, 22.xi.1949, E. F. Riek, 1 ♂; Broken Hill, 10 miles N. of, 20–23.xi.1949, E. F. Riek, 3 ♂♂, 1 ♀. SOUTH AUSTRALIA: Adelaide, 16.x.1946, H. M. Cane, 1 ♂; Adelaide, 8.xi.1946, H. M. Cane, 1 ♂. TASMANIA: Hobart, 19.xi.1916, C. E. Cole, 1 ♂, 1 ♀; Hobart, 2.xii.1917, C. E. Cole, 1 ♂, 2 ♀♀; Hobart, 28.xii.1947, E. F. Riek, 1 ♂; Upper Blessington, 16.iii.1934, N. J. B. Plomley, 14 ♀♀.

ONCODES PYGMAEUS White, ♂, ♀

Oncodes pygmaeus White, 1914, Pap. Roy. Soc. Tasm. 1914: 72.

The author is not convinced that this species is different from *flavescens* (which is a synonym of *fortnumi*) but a series of more than 160 females shows that some differences, though small, are constant: (1) average size of *pygmaeus* is smaller, although some specimens can be as large as the smallest specimens of *flavescens*; (2) abdomen of *pygmaeus* always uniformly coloured or with only the slightest hints of lighter fasciae along the hind margins of tergites; in *flavescens* the whitish fasciae are always present and well developed; (3) legs in *pygmaeus* are more dirty yellow than in *flavescens*; (4) knees in *flavescens* usually narrowly dark. These differences probably but not necessarily indicate two distinct species. Five pairs collected in copula also represent typical *pygmaeus*, but not mixed males and females of two species.

All females were collected by Mr. N. J. B. Plomley, with a series of more than 115 specimens of males, on 6. iii. 1934, at Upper Blessington, Tas. With them were collected also seven males and 61 females of *flavescens*. It is suggested that there are two species occurring in that area. The author also collected one female at Canberra on 9. x. 1948.

From the description of *flavescens* it is evident that White did not separate these two forms, but his *flavescens* is doubtlessly only a synonym of one of Westwood's species. White overlooked the work of Westwood, and in his review of Tasmanian Cyrtidae did not mention, for example, even *O. tasmanica* Westw.

Type, female, from Launceston, Tas. (F. M. Littler).

ONCODES ATER White, ♂, ♀

Oncodes ater White, 1914, Pap. Roy. Soc. Tasm. 1914: 72.

Female.—Entire body black, strongly shining; only tibiae and tarsi yellow. Both spiracles whitish. Wing hyaline, with a very well-developed vein separating the lower basal cell from the last posterior. All usual rudiments of veins are present. Anal cell not closed: if the 2 veins at its apex were produced the cell would be narrowly open. Lower calypter greyish milky, with brownish rim. Halteres dark. Hind metatarsus about as long as the combined length of the 3 following joints of the tarsi. Hairs on body dense, yellowish.

Femora very thin, cylindrical, quite unswollen and about as thick as the tibiae. Lower basal cell very narrow, at broadest point as broad as the distance from costa to radial stem; vein closing this cell is short, nearly straight.

Length of body 7.5 mm, of wing 6 mm.

The female specimen is in the Department of Entomology, University Museum, Oxford. The specimen has labels: (1) "Tasmania"; (2) "Australia Jamison 1079"; (3) "*Ogcodes ater* Wandek., MSS of Benno Wandolleck, in Berlin, 1899", and an asterisk, usually indicating the type.

This species belongs to the group with very thin legs (closely related to *O. tenuipes*, sp. nov.); all femora are nearly cylindrical, and about as broad as the tibiae, which are also parallel-sided, and not broadening towards the apices. Lower basal cell at broadest point is distinctly narrower than the anal cell. Hairs on mesonotum very dense, brownish, about as long as the diameter of the anterior spiracle. Last metatarsus is as long as 3 following joints combined. Lower calypter darkish, with black rim. Hairs on abdomen sparse, shorter than on mesonotum. Claws in both sexes very short. Sexes differ only in sexual characters.

Specimens examined.—VICTORIA: Ringwood, 22.x.1950, F. E. Wilson, 1 ♂, 1 ♀ (very well preserved, in Wilson Collection); Woodend, 24.x.1937, F. E. Wilson, 1 ♂. TASMANIA: 1 ♀.

Type, male, from Bridport, Tas, 30.x.1913, F. M. Littler. This species has not hitherto been recorded.

ONCODES TENUIPES, sp. nov., ♂

Belongs to the group in which the lower basal cell is separated from the last posterior cell by a distinct but pale vein.

Size, shape, and colour as in *fortnumi*, but the structure of legs and abdomen is very peculiar. Fore femora very thin, only slightly swollen, nearly parallel-sided, and about as thick as the fore tibiae, which are cylindrical. Mid femora have about the same proportions; hind femora are thicker than tibiae only in their apical half, in their basal half the hind femora are thinner than the tibiae, which are cylindrical. Metatarsi about as long as the combined length of the 3 following joints. All claws extremely short.

Abdomen dark brown, hind borders at sides of 3rd and 4th tergites narrowly reddish. Structure of the 5th tergite is very peculiar as it is excavated in profile, and the 3rd and 4th tergites are humpbacked; in most species the contour of the tergites is a regular curve, in *tenuipes* each of first 4 tergites is slightly swollen and after the 4th, the contour goes sharply downwards.

Another peculiarity is the absolute smoothness of the central half of the 5th tergite. It is polished, shining, without any traces of hairs, but two lateral fourths have rather dense, erect hairs.

Legs reddish yellow. Wings and venation as in *fortnumi*. Hairs on body rather long. Frons is flush, extremely small. The lower basal cell at broadest point distinctly narrower than the anal at the same point.

Length of body 6.5 mm, of wing 5 mm.

Specimens examined.—VICTORIA: 1 ♂ (type). NEW SOUTH WALES: Blackheath, 29.ix.1934, D. F. Waterhouse, 1 ♂ (C.S.I.R.O. Mus., Canberra). QUEENSLAND: Gayndah, Masters, 1 ♂ (Aust. Mus., Sydney).

Type in Australian Museum, Sydney.

The last two species examined differ from the type mostly in features of colour. Both of them also have a peculiarity which is not evident in the type, because its wings are stuck to the sides of the abdomen. In both specimens the hairs on the sides of 2nd, 3rd, and 4th tergites are distinctly shorter than in the middle area and regularly depressed towards the middle line; this depression is so symmetrical and similar in both specimens that it can be regarded as characteristic. The specimen from Blackheath, N.S.W., is of the same size as the type, but all femora are dark brown, exactly the same colour as the abdomen, which is uniformly dark brown. Hairs on body nearly whitish, therefore the depressed hairs on the abdomen have a slightly silvery shine. The peculiar form of 5th tergite is not so markedly developed as in the type. The specimen from Gayndah, Qld., is distinctly smaller than the type, and resembles very much the specimen from Blackheath, the main difference is that the legs and abdomen are not so dark, but the specimen is probably an old one and has not retained its natural colour well.

Among the material of the National Museum, Melbourne, there is also one male from Frankston, Vic., very similar to the specimen from Blackheath.

ONCODES NIGRINERVIS White

Oncodes nigrinervis White, 1914, Pap. Roy. Soc. Tasm. 1914: 71.

The author has not seen this species.

ONCODES HIRTIFRONS, sp. nov., ♂, ♀

Belongs to the group with a lower basal cell separated from the posterior cell by a distinct vein.

Ocellar tubercle prominent, with 2 distinct ocelli. Frons in upper part with light hairs. Antennae brownish. Head in profile with upper arc distinctly flattened, not circular. Frons in profile nearly flush.

Thorax black, shining, with dense, comparatively long, light hairs; their length is about three times the diameter of the anterior spiracle. Wings quite hyaline, with yellow veins; a vein separating the lower basal cell from the last posterior cell is quite distinct, S-like; anal cell at apex very narrow. Lower calypter slightly greyish, brownish along the edge. Legs yellow. Femora rather massive, long-haired, metatarsi thin, cylindrical, not swollen.

Male abdomen predominantly yellow. First tergite (scarcely noticeable) black; 6th brown; 2nd dark brown, but with whitish hind margin and yellow lateral triangles at hind margin; 3rd only with dark fascia along the anterior margin, with posterior half and sides yellow; 4th with only traces of the dark marking at anterior margin. There are also small, dark triangles on tergites 3-5 at the sides at the junction with the sternites. Underside predominantly yellow, with darker fasciae at anterior margin of sternites.

Female abdomen is dark brown, with narrow whitish hind margins, underside predominantly yellow.

Hairs on tergites in female shorter than in male and distributed regularly. In male on posterior half of 4th tergite and on anterior half of 5th the hairs are much shorter than at the sides.

Length of body 8 mm, of wing 6.5 mm.

Specimens examined.—NEW SOUTH WALES: Mt. Kosciusko, 6500 ft, 31.xii.1933, Mackerras, 1 ♂ (type); Mt. Kosciusko, 1.ii.1930, R. J. Tillyard, 1 ♂, 1 ♀; Mt. Kosciusko, 6.i.1929, A. Musgrave, 6 ♂♂, 3 ♀♀; Mt. Kosciusko, 16.ii.1952, K. R. Norris, 1 ♀. TASMANIA: Perth, 2.ii.1949, E. F. Riek, 1 ♀.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra. Cotypes in Australian Museum, Sydney.

ONCODES CANBERRANUS, sp. nov., ♂

Belongs to the group with a vein separating the lower basal cell (*M*) from the posterior cell.

Head black, hemispherical in profile, with frons extremely short and virtually absent, being only as large as the basal joint of antennae, bare. Occiput with yellowish, rather dense hairs.

Thorax black but with orange markings: humeral and postalar calli with 2 large lateral spots behind the humeral calli, and the whole upper parts of the sides of the thorax. Hairs rather long, yellowish, distinctly longer than the diameter of anterior spiracle (2–3 times). Calyptae dark, with yellowish hairs. Wings slightly yellowish, with very narrow anal cell nearly closed at apex and a very well-developed vein separating the lower basal cell from the last posterior. Legs orange-yellow, with coxae distinctly thicker than tibiae. Hind metatarsus shorter than 3 following joints combined, no dilatation at apex of hind tibiae.

Abdomen uniformly orange, with broad dark fasciae in the central part of tergites; these bands fail to reach the hind margin of the tergites by one-third of the length of the tergite, and are also shortened laterally; hairs yellowish, erect, shorter than on mesonotum.

Length of body 7 mm, of wing 5.5 mm.

Specimen examined.—AUSTRALIAN CAPITAL TERRITORY: Condor Creek, 15.xi.1929, G. F. Hill, 1 ♂ (type).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

ONCODES GLOMEROSUS, sp. nov., ♂

Belongs to the *fortnumi-ater* group.

Head black, very prominent. Frons small, but a little longer than the ocellar tubercle. Occiput nearly bare.

Mesonotum deep black, shining in central part, hairs short, black, laterally much longer, yellowish.

Wings quite hyaline, veins pale yellowish, venation as in *canberranus*. Calypter dark rimmed, whitish, with narrow transparent area at margin. Halteres dark. Legs predominantly black, yellowish only at apices of femora, above, and slightly on the apices of tibiae. Hairs on legs yellowish. Femora only a little thicker than tibiae.

Abdomen deep black, very shining. Sides of 2nd-5th tergites with bright yellow (or orange) triangular spots joined by similar narrow fasciae on the hind margin. Hairs yellowish.

Length of body 5.5 mm, of wing 5 mm.

Specimens seen.—NEW SOUTH WALES: Spencer's Creek, Mt. Kosciuszko, 18.10.1951, E. Troughton, 1 ♂ (type); Guyra, 21.1.1949, A. Dyce, 1 ♂.

Type in the Australian Museum, Sydney.

ONCODES LUCIDUS, sp. nov., ♂.

Closely related to *glomerosus*, but easily distinguishable by having long yellowish hairs of equal size on whole mesonotum, completely black legs, and the light yellow markings of the abdomen much narrower and less bright than in *glomerosus*. Legs comparatively weak. Occiput shortly haired. Anal cell closed well before the hind margin, i.e. long petiolated. Axillar cell extremely broad.

Length of body 5 mm, of wing 4 mm.

Specimen examined.—NEW SOUTH WALES: Mt. Kosciuszko, 12.11.1954, D. F. Waterhouse, 1 ♂ (type).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

REFERENCES

- BRUNETTI, E. (1926).—New and little-known Cyrtidae. *Ann. Mag. Nat. Hist.* (9) **18**: 590-606.
- ERICHSON, W. F. (1840).—"Entomographia", Vol. 1. p. 163.
- FROGGATT, W. W. (1907).—"Australian Insects." p. 298. (Wm. Brooks: Sydney.)
- HARDY, G. H. (1916).—Notes on Tasmanian Diptera and descriptions of new species, etc. *Pap. Roy. Soc. Tasm.* for **1916**: 267-8.
- HARDY, G. H. (1918).—Notes on Tasmanian Diptera and descriptions of new species. *Pap. Roy. Soc. Tasm.* for **1917**: 60-1.
- HARDY, G. H. (1922).—Australian Bombyliidae and Cyrtidae (Diptera). *Pap. Roy. Soc. Tasm.* for **1921**: 77-8.
- HARDY, G. H. (1940).—Miscellaneous notes on Australian Diptera. VII. On body colour and on species of Tabanidae, Cyrtidae and Asiloidea. *Proc. Linn. Soc. N.S.W.* **65** (5-6): 486-7.
- MACQUART, J. (1838a).—"Diptères Exotiques Nouveaux ou Peu Connus." Vol. 1. Pt. 2. pp. 165-75.
- MACQUART, J. (1838b).—Hist. Nat. Insectes. Diptères. Vol. 2. pl. 21, figs. 5a, 5b.
- MACQUART, J. (1840).—"Diptères Exotiques Nouveaux ou Peu Connus." Vol. 2. Pt. 1. pl. 1, fig. 2.
- PARAMONOV, S. J. (1955).—New Zealand Cyrtidae (Diptera) and the problem of the Pacific island fauna. *Pacif. Sci.* **9**: 16-25.
- PLOMLEY, N. J. B. (1947a).—Biology of the Cyrtidae. *Rec. Q. Vict. Mus.* for 1946. **2**: 23-30.
- PLOMLEY, N. J. B. (1947b).—On the external genitalia of *Oncodes basalis* Walk. *Rec. Q. Vict. Mus.* for 1946. **2**: 17-22.
- SACK, P. (1936).—In "Die Fliegen der palaearctic Region". (Ed. E. Lindner.) Vol. 4. Pt. I. Sect. 21. pp. 1-36.
- SÉGUY, E. (1951).—In "Traité de Zoologie". (Ed. Grassé.) Vol. 10. pp. 647-8.
- WALKER, F. (1852).—"Insecta Saundersiana, Diptera." Pt. 3. p. 203.
- WANDOLLECK, B. (1906).—A new species Cyrtidae (Diptera) from N. Queensland, bred by F. P. Dodd. *Trans. Ent. Soc. Lond.* **1906**: 131-2.

Westwood, J. O. (1848).—Descriptions of some new exotic species of Acroceridae (*Vesiculosia* Latr.), a family of dipterous insects. *Trans. Ent. Soc. Lond.* **1848**: 97.

Westwood, J. O. (1876).—Notae Dipterologicae, No. 2. Descriptions of new genera and species of the family Acroceridae. *Trans. Ent. Soc. Lond.* **1876**: 516–17.

White, A. (1914).—The Diptera Brachycera of Tasmania. I. *Pap. Roy. Soc. Tasm.* for **1914**: 69–72.

LIST OF SPECIES

Genus <i>Leucopsina</i> Westw.	524	<i>castaneus</i> Brun.	539
<i>olyneroides</i> Westw.	524	<i>darwinii</i> Westw.	535
Genus <i>Panops</i> Lam.	525	<i>deserticola</i> , sp. nov.	538
<i>baudini</i> Lam.	526	<i>doddi</i> Wand.	537
<i>conspicuus</i> (Brun.)	529	<i>fortnumi</i> Westw.	540
<i>flavipes</i> Latr.	527	<i>fumatus</i> Frogg.	539
<i>flavipes</i> var. <i>burnsi</i> , var. nov.	529	<i>glomerosus</i> , sp. nov.	544
Genus <i>Pterodontia</i> Gray	529	<i>hirtifrons</i> , sp. nov.	543
<i>darvsi</i> , sp. nov.	531	<i>insignis</i> Brun.	538
<i>melli</i> Erichs.	530	<i>lucidus</i> , sp. nov.	545
<i>variegata</i> White	531	<i>nigrinervis</i> White	543
Genus <i>Oncodes</i> Latr.	531	<i>pusillus</i> , sp. nov.	539
<i>armstrongi</i> , sp. nov.	537	<i>pygmaeus</i> White	541
<i>ater</i> White	541	<i>tenuipes</i> , sp. nov.	542
<i>basalis</i> (Walk.)	534	<i>variegatus</i> Brun.	539
<i>camberranus</i> , sp. nov.	544	<i>victoriensis</i> Brun.	536
		<i>waterhousei</i> , sp. nov.	537
		<i>wilsoni</i> , sp. nov.	538

INDEX

	PAGE
Acroceridae, Australian, Review of	521
<i>Aelurostrongylus abstrusus</i> , Observations on the Life History of	188
Aganippine Trapdoor Spiders, Biology of	402
Amphibia, Australian, Studies in. I	30
<i>Anoplognathus</i> Leach, a Revision of the Ruteline Genus	88
<i>Austroicetes</i> Uv., a Cytotaxonomic Study of the <i>pusilla</i> Group of Species in the Genus	56
Barton Browne, L.—	
The Effect of Light on the Mating Behaviour of the Queensland Fruit Fly <i>Strumeta tryoni</i> (Frogg.)	145
An Investigation of the Low Frequency of Mating of the Queensland Fruit Fly	159
Biology of Aganippine Trapdoor Spiders	402
Blowfly, Australian Sheep, Utilization and Digestion of Carbohydrates by	164
Bornemissza, G. F.—	
An Analysis of Arthropod Succession in Carrion and the Effect of its Decomposition on the Soil Fauna	1
Carne, P. B.—	
A Revision of the Ruteline Genus <i>Anoplognathus</i> Leach (Coleoptera: Scarabaeidae)	88
Cat Lungworm, Observations on the Life History of	188
Chinnick, L. J.—	
See White, M. J. D.	338

	PAGE
Clark, A. M.—	
Hybridization between <i>Drosophila setifemur</i> and <i>D. spinofemora</i>	216
Cleland, K. W.—	
See Reid, B. L.	223
<i>Climacteris</i> Temminck, Variation and Speciation in the Genus	474
<i>Crinia</i> Tschudi, the Genus, in South-western Australia	30
Cytotaxonomic Study of the <i>pusilla</i> Group of Species in the Genus <i>Austroicetes</i> Uv.	56
<i>Damalinea oris</i> (L.).—	
Oviposition Behaviour	19
Distribution of the Eggs of, on the Sheep	173
<i>Damalinea equi</i> (Denny), Distribution of the Eggs of, on the Horse	183
<i>Drosophila setifemur</i> and <i>D. spinofemora</i> , Hybridization between	216
Dyce, A. L.—	
See Lee, D. J.	355
Epididymis, Rat, Histology of	223
Flies, Blood-sucking (Diptera), and Myxomatosis Transmission in a Mountain Environment in New South Wales	355
Fruit Fly, Queensland.—	
Effect of Light on the Mating Behaviour of	145
Investigation of the Low Frequency of Mating of	164
Grasshopper, Cytogenetics of. I, II, III, IV	285, 305, 338, 348

- | | PAGE | | PAGE |
|---|------------------|---|--------------------|
| Griffing, B.— | | Madge, P. E.— | |
| <i>See</i> White, M. J. D. | 305 | The Ecology of <i>Oncopera fasciculata</i> (Lepidoptera: Hepialidae) in South Australia. IV. Fluctuations in Numbers during 1948–1955 and an Analysis of their Causes | 196 |
| <i>Haematopinus asini</i> (L.), Distribution of the Eggs of, on the Horse | 183 | Main, Barbara Y.— | |
| <i>Hapatesus</i> Candèze and <i>Toorongus</i> , gen. nov., Taxonomy of | 496 | Biology of Aganippine Trap-door Spiders (Mygalomorphae: Ctenizidae) | 402 |
| Hybridization between <i>Drosophila setifemur</i> and <i>D. spinofemora</i> | 216 | Main, A. R.— | |
| Keast, A.— | | Studies in Australian Amphibia. I. The Genus <i>Crinia</i> Tschudi in South-western Australia and some Species from South-eastern Australia | 30 |
| Variation and Speciation in the Genus <i>Climacteris</i> Temminck (Aves: Sittidae) | 474 | <i>Moraba scurra</i> , Cytogenetics of, I, II, III, IV | 285, 305, 338, 348 |
| Kentromorphic Phases in Three Species of Phasmatodea | 247 | Murray, M. D.— | |
| Key, K. H. L.— | | The Distribution of the Eggs of Mammalian Lice on their Hosts. I. Description of the Oviposition Behaviour | 13 |
| Kentromorphic Phases in Three Species of Phasmatodea | 247 | II. Analysis of the Oviposition Behaviour of <i>Damalinia ovis</i> (L.) | 19 |
| <i>See also</i> White, M. J. D. . . . | 56 | III. The Distribution of the Eggs of <i>Damalinia ovis</i> (L.) on the Sheep | 173 |
| Lee, D. J., Dyce, A. L., and O'Gower, A. K.— | | IV. The Distribution of the Eggs of <i>Damalinia equi</i> (Denny) and <i>Haematopinus asini</i> (L.) on the Horse | 183 |
| Blood-sucking Flies (Diptera) and Myxomatosis Transmission in a Mountain Environment in New South Wales | 355 | Myxomatosis Transmission in a Mountain Environment in New South Wales, Blood-sucking Flies (Diptera) and | 355 |
| Lice, Mammalian, Distribution of the Eggs of, on their Hosts. I, II, III, IV | 13, 19, 173, 183 | | |
| <i>Lucilia cuprina</i> , Utilization and Digestion of Carbohydrates by . . | 164 | Neboiss, A.— | |
| Lungworm, Cat, Observations on the Life History of | 188 | The Genera <i>Hapatesus</i> Candèze and <i>Toorongus</i> , gen. nov. (Coleoptera: Elateridae) | 496 |
| Mackerras, M. Josephine.— | | O'Gower, A. K.— | |
| Observations on the Life History of the Cat Lungworm, <i>Aelurostrongylus abstrusus</i> (Railliet, 1898) (Nematoda: Metastrongylidae) | 188 | <i>See</i> Lee, D. J. | 355 |

	PAGE
<i>Oncopera fasciculata</i> (Walker), Ecology of, in South Australia. IV	196
Paramonov, S. J.— A Review of Australian Acro- ceridae (Diptera)	521
Phasmatodea, Kentromorphic Phases in Three Species of	247
Rat Epididymis, Histology of	223
Reid, B. L., and Cleland, K. W.— The Structure and Function of the Epididymis. I. The Histology of the Rat Epididymis	223
Sheep Blowfly, Australian, Utiliza- tion and Digestion of Carbo- hydrates by	164
Spiders, Trapdoor, Biology of	402
<i>Strumeta tryoni</i> (Frogg.).— Effect of Light on the Mating Behaviour of	145
Investigation of the Low Fre- quency of Mating of	164

	PAGE
<i>Toorongus</i> , gen. nov., and <i>Hapatesus</i> Candèze (Coleoptera: Elateridae), Taxonomy of	496
Trapdoor Spiders, Aganippine, Biology of	402
Webber, L. G.— Utilization and Digestion of Carbohydrates by the Australian Sheep Blowfly <i>Lucilia cuprina</i>	164
White, M. J. D.— Cytogenetics of the Grasshopper <i>Morabascurra</i> . I. Meiosis of Inter- racial and Interpopulation Hy- brids	285
II. Heterotic Systems and their Interaction	305
III. Distribution of the 15- and 17-chromosome Races	338
IV. Heterozygosity for "Elastic Constrictions"	348
White, M. J. D., and Key, K. H. I.— A Cytotaxonomic Study of the <i>pusilla</i> Group of Species in the Genus <i>Austroicetes</i> Uv. (Orthop- tera: Acrididae)	56

NOTICE TO CONTRIBUTORS

1. **GENERAL.**—Papers will be considered for publication irrespective of the organization to which the authors are attached. Intending contributors, in preparing papers for submission, should follow the general style adopted in this Journal. A "Guide to Authors" may be obtained on application to the Editor. Papers, which should be written as concisely as possible, should be double-space typed on one side of the paper only and with liberal side margins. Every page, including those carrying tables and illustrations, should be numbered. Lengthy manuscripts should be accompanied by a table of contents with headings appropriately numbered. The organization to which the author is attached should be indicated in a footnote.

The original typescript and one carbon copy should be forwarded.

2. **TAXONOMIC PAPERS.**—Except under very special circumstances, taxonomic papers must deal comprehensively with a natural group of animals. A pamphlet entitled "Recommendations for the Preparation of Zoological Papers with Special Reference to Taxonomy" may be obtained on application to the Editor.
3. **SUMMARY.**—A short summary, which may be paragraphed, should precede the introduction to the paper. It should be of an informative character and written in such a way that it can be used by abstracting journals without amendment.

4. **REFERENCES.**—References are to be cited in the text by the year of publication, e.g. Kennedy (1939), and are to be arranged alphabetically, giving the author's name and initials followed by the year of publication, title of the paper (if desired), title of the periodical, volume, and pages, thus:

Kennedy, J. S. (1939).—The behaviour of the desert locust (*Schistocerca gregaria* (Forsk.)) (Orthoptera) in an outbreak centre. *Trans. R. Ent. Soc. Lond.* 89: 385–542.

Abbreviations of titles of periodicals should conform to those used in "A World List of Scientific Periodicals."

5. **ILLUSTRATIONS.**—Line drawings should be made with indian ink on white drawing paper (preferably bristol board), tracing paper, blue linen, or graph paper. Only blue or pale grey ruled graph paper should be used. The lines should be sufficiently thick and the lettering and numbering sufficiently large to allow of reduction to a page size of $7\frac{3}{4}$ by 5 in. without loss of detail. Originals of line drawings should be submitted but, where feasible, photographic copies of the originals should also be forwarded.

Half-tone photographs, which should be included only where essential, should be on glossy paper and show as much contrast as possible.

6. **REPRINTS.**—Individual authors receive 40 copies of each paper free, two authors receive 30 each, and three or more authors receive 20 each, but additional copies may be purchased provided they are ordered by the author when returning the corrected proofs.

CONTENTS

	PAGE
Blood-sucking Flies (Diptera) and Myxomatosis Transmission in a Mountain Environment in New South Wales. By D. J. Lee, A. L. Dyce, and A. K. O'Gower	355
Biology of Aganippine Trapdoor Spiders (Mygalomorphae : Ctenizidae). By Barbara Y. Main	402
Variation and Speciation in the Genus <i>Climacteris</i> Temminck (Aves : Sittidae). By A. Keast	474
The Genera <i>Hapatesus</i> Candèze and <i>Toorongus</i> , gen. nov. (Coleoptera : Elateridae). By A. Neboiss	496
A Review of Australian Acroceridae (Diptera). By S. J. Paramonov	521
Index to Volume 5	547

